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INTRODUCTION

Although bats have fascinated man for centuries, many of the osteological and muscular specializations that enable these animals to fly have not been studied. Certain aspects of the life histories of bats have been carefully investigated, and the biology of some bats is well understood, but little is known of the foraging habits or of the details of flight or terrestrial locomotion in many bats. The primary objectives of the study here reported on were: (1) to investigate locomotion in bats by means of field studies on the foraging and roosting habits of three North American bats, the western mastiff bat (*Eumops perotis,* Molossidae), the cave myotis (*Myotis velifer,* Vespertilionidae), and the leaf-nosed bat (*Macrotus californicus,* Phyllostomidae); (2) to describe and compare the appendicular myology and osteology of these bats; (3) to ascertain the functional significance of their basic osteological and myological adaptations for flight; (4) to find how the differences between the habits of the three bats under study are reflected in their appendicular morphology; (5) to compare some of the major morphological adaptations for flight in bats and birds.

The bats listed above were chosen for study because they differ from one another widely with respect to habits and morphology and seem to illustrate much of the diversity occurring between bats of the suborder Microchiroptera. It was thought that anatomical differences between the three kinds of bats mentioned might be ascertained more readily and might be more indicative of contrasting trends within the suborder than would less striking differences between closely related animals.

Except for scattered observations at earlier dates, field work on this study began in June 1953, and was also carried out in parts of the summers of 1954 and 1957. A total of roughly 60 days in the field was devoted to this project. The laboratory section of the study was started in December of 1952 and was terminated in December 1957.

In the nineteenth century a number of papers were published on the anatomy of bats, but the number of species covered by these reports was small. Among the authors who investigated bat anatomy in this period were Cuvier (1800-1805), Kolenati (1857), and Humphrey (1869). Macalister (1872) studied the myology of 19 species of bats representing the families Pteropidae, Rhinolophidae, Megadermidae, Phyllostomidae and Vespertilion-

idae, and corrected numerous errors made by earlier workers. Little attention has been given to the myology of bats since Macalister's paper was published and it remains a major reference on the subject. Eisentraut (1936), on the basis of moving picture filmstrips of flying bats, carefully described the wing movements made by bats in various types of flight. The life history of *Eumops perotis* has been considered by Howell (1920a) and Krutzsch (1955). The habits of *Myotis velifer* have been reported on by Stager (1939) and Twente (1955). Only scattered notes have been published on the behavior of *Macrotus californicus* and its life history is poorly known.

I am pleased to acknowledge the help of Professor E. Raymond Hall, under whose guidance this study was conducted. For important help in various ways I extend my sincere thanks to Mr. Sydney Anderson, Dr. George W. Byers, Dr. A. Byron Leonard, Dr. Charles Pitrat, and Dr. Robert W. Wilson, all of the University of Kansas, and to Dr. Philip H. Krutzsch of the University of Pitttsburgh, Mr. J. R. Alcorn of Fallon, Nevada, Mrs. G. M. Richards of Vidal, California, and to my wife, Hazel A. Vaughan. All photographs and drawings are by the author.

Materials and Methods

Most of my field work was done in southern California, in Los Angeles, San Bernardino, Riverside and San Diego counties. Some additional observations were made on *Eumops* in Merced and Tuolumne counties, California. The field studies were carried out mainly in localities away from human habitation, and were supplemented by observations of bats in the laboratory. Photographs were taken in the field and in the laboratory with an Eastman Bantam Special and a Heiland Strobonar electronic flash. Bats were obtained by shooting, by the use of nets, and by stretching wires about one inch above the surfaces of ponds. Specimens of several kinds of bats other than those serving as the central subject of this report were taken in various parts of Kansas, and in Washington county, Utah, and were used as comparative material.

The animals saved for anatomical investigations were preserved in the field in a solution of one part formalin to eight parts water. An opening was made into the visceral cavity of each specimen to facilitate rapid preservation, and some specimens of *Eumops* were injected. After several weeks, generally when the specimens were brought to the laboratory, they were transferred to a solution of 70 percent alcohol. All of the dissections were made with the aid of a low power binocular microscope equipped with a 6.6X, a 13X, and a 30X objective. A number of bats of each of the three species under study were dissected. No volumetric determinations on the muscles were made. For any one muscle, individual variation seemed to be slight in size, in place of origin and in place of insertion.

Skeletons used are in the University of Kansas Museum of Natural History. The drawings of bones are from the following specimens: *Eumops perotis,* 73128, 73214; *Myotis velifer,* 52465; *Macrotus californicus,* 52458. The fol-

lowing preserved specimens were used and are mostly in the above named museum; specimens marked TV are in the collection of the writer.

Chilonycteris personata Wagner—19 mi. E San Andrés Tuxtla, 1000 ft., Veracruz, 1 (KU 24636).

Pteronotus davyi fulvus (Thomas)—19 mi. E San Andrés Tuxtla, 1000 ft., Veracruz, 1 (KU 24646).

Macrotus mexicanus bulleri H. Allen—12 mi. N and 3 mi. W Los Mochis, Sinaloa, 1 (KU 60609).

Macrotus californicus Baird—35 mi. N Blythe, Riverside Co., California, 18 (KU 76538-76555).

Glossophaga soricina leachii (Gray)—2 mi. ESE Tepanatepec, Oaxaca, 1 (KU 70492).

Choeronycteris mexicana Tschudi—3 mi. E Raboso, Puebla, 1 (KU 67382).

Leptonycteris nivalis nivalis (Saussure)—¼ mi. W Aduana, 1600 ft., Sonora, 1 (KU 25005).

Artibeus hirsutus Anderson—¼ mi. W Aduana, 1600 ft., Sonora, 1 (KU 25072).

Myotis velifer brevis Vaughan—35 mi. N Blythe, Riverside Co., California, 18 (KU 76556-76573).

Eptesicus fuscus fuscus (Palisot de Beauvois)—1 mi. SE Leavenworth, Leavenworth Co., Kansas, 1 (KU 76574).

Lasiurus cinereus cinereus (Palisot de Beauvois)—12½ mi. N and 5½ mi. W St. Francis, Cheyenne Co., Kansas, 1 (KU 52432).

Tadarida brasiliensis (Saussure)—8 mi. NE Ocotlán, 5100 ft., Jalisco, 5 (KU 32007, 32009, 32011, 32012, 32014).

Chaerophon luzonus Hollister—Luzon, Philippine Islands, 1 (KU 10524).

Tadarida molossa (Pallas)—Zion National Park, Washington Co., Utah, 3 TV 731-733); 2 mi. E La Palma, Michoacán, 10 (KU 38291, 38296, 38298, 38301-38305, 38307).

Eumops perotis californicus (Merriam)—*Los Angeles Co.:* 3 mi. S and 1 mi. W Newhall, 1 (KU 76575); ¾ mi. NW Chatsworth, 1 (KU 76576); 1 mi. W Chatsworth, 1 (KU 76577). *Riverside Co.:* 4 mi. SW Lakeview, 3 (KU 76578-76580). *San Diego Co.*: 1½ mi. N Barrett, 5 (KU 76581-76582; TV 709, 710, 712).

Molossus nigricans Miller—1 mi. N Sebana Grande, Managua, Nicaragua, 1 (KU 71033).

Molossus bondae J. A. Allen—Turrialba, Costa Rica, 1 (KU 57151).

Molossus obscurus E. Geoffroy Saint-Hilaire—Ilha Madre de Deus, Bahia, Brazil, 3 (KU 41153-41155).

Molossus coibensis J. A. Allen—3 mi. SW Managua, Nicaragua, 1 (KU 71007).

REMARKS ON THE BATS STUDIED

The western mastiff bat (*Eumops perotis*) is a member of the family Molossidae. This family occurs mainly in the tropical, subtropical and desert regions of both hemispheres. The range of the species in the southwestern United States extends as far north as central California; *E. perotis* has also been recorded from Texas, the state of Sonora, Mexico, Cuba, and parts of northern South America. In the southwestern United States this bat inhabits arid desert regions, grassland areas, sections dominated by chaparral, and occurs locally in the yellow pine belt of the Sierra Nevada Mountains of California. (The presence of *E. perotis* in the latter

area is hitherto unreported. I have heard the distinctive cries of mastiff bats on many occasions in Yosemite and Hetch Hetchy Valleys, Yosemite National Park, and there are several specimens in the Yosemite National Park Museum.) This is a large bat of roughly 155 mm. to 185 mm. total length. The broad ears face ventrolaterad and are connected across the top of the snout. The flight membranes are tough and leathery; the wings are long and narrow, and approximately the distal half of the tail extends beyond the uropatagium. The color of the pelage is dark gray or brownish gray.

The cave myotis (*Myotis velifer*) belongs to the family Vespertilionidae; this family is nearly world-wide in distribution except in arctic regions. This bat occurs from south-central Kansas through the southwestern United States, and south to Guatemala. It is known also from the southern tip of Baja California. The cave myotis inhabits tropical, subtropical and temperate regions. It is a small "mouse eared" bat, having a total length of from approximately 92 mm. to 105 mm. The pelage is usually pale brown; the wings are broad and the uropatagium extends to the end of the tail.

The leaf-nosed bat (*Macrotus californicus*) belongs to the New-World family Phyllostomidae. The range of this family includes the warmer parts of the southwestern United States, Mexico, Central and South America, and the Bahama Islands. This species inhabits the arid deserts of the southwestern United States as far north as southern Nevada, south to Baja California and Sonora, Mexico. The leaf-nosed bat is of medium size, with a total length of roughly 93 mm. to 103 mm., and is distinctive in appearance. The ears are large and are connected across the forehead. There is a small nose-leaf, and the body is pale grayish brown dorsally with whitish underparts. The flight membranes are thin and delicate; the wings are broad and the tail is slightly shorter than the long hind limbs and extends several millimeters beyond the uropatagium.

LOCOMOTOR BEHAVIOR

Some understanding of both terrestrial and aerial locomotion is necessary in order to interpret correctly the morphology of the bats under study. Because terrestrial locomotion is important only in connection with roosting in most insectivorous bats, and aerial locomotion is used primarily in foraging, a consideration of the foraging and roosting habits of each of the bats is important in a study of their functional morphology.

Eumops perotis

Roosting Habits and Terrestrial Locomotion

Most of my observations on free living individuals of this species were made in the chaparral belt of coastal southern California. I examined 22 roosting sites that were being used or had recently been used by *Eumops*. Of these sites only eight were used by colonies of bats; most of the other roosting sites were used by single bats, whereas a few roosts harbored groups of two or three bats.

Away from human habitations, this bat generally seeks diurnal refuge in crevices in rocks that form vertical or nearly vertical cliffs, or that are situated on steep slopes. All of the occupied crevices that I examined were more than a foot deep and had entrances that were at least two inches wide and six inches long and were at the bottoms or sides of the crevices. A larger crevice is preferred, however, and some of the slitlike openings were five to 10 feet long. Several crevices that were occupied by colonies of *Eumops* were at least 10 feet deep; the total depths of these larger crevices were not ascertained. Large, exfoliating slabs of rock seemed most often to form crevices suitable for these bats. Because granitic rocks and consolidated sandstones are likely to weather by exfoliation and form deep, vertical crevices suitable for retreats for *Eumops,* this bat is most common in broken terrain where extensive exposures of these rocks occur.

The roosting sites examined all had several characteristics in common. All of the sites had moderately large openings that could be entered from below. Measured through the anterior part of the thorax, the thickest part of its body, *Eumops* is roughly one inch thick. This bat occupies crevices the openings of which are at least twice as wide as its body, probably because entrances of this size may be entered rapidly and easily. The entrances are usually horizontally oriented and face downward. According, these bats can leave their roosts by simply dropping from the crevice, and they can alight by swooping up into it from below. The entrances to several of the roosts were more than twelve feet long. All of the roosts were crevices that became narrow enough at some point to enable the bats to wedge themselves into the space and have their dorsal and ventral surfaces against the rock surfaces. On several occasions bats were frightened and forced themselves into narrow spaces so tightly that when shot and killed the bats remained in place.

Characteristically *Eumops* roosts in crevices that are high above the ground and have unobstructed approaches. Howell, who studied colonies of *Eumops* in buildings in southern California, stated (1920a:112) that these bats always choose a roost below which there is a drop of at least 20 feet, so that the bats can, by dropping from the roost, gain flying speed. I agree with Howell that *Eumops* chooses high roosting places. All the roosts found by me were in rocks in broken, hilly or mountainous country, where steeply sloping terrain provided additional space in which the bat could gain speed. These roosts were situated from six to 40 feet above the slope, and a nearly straight drop of at least six feet was always available beneath the crevice. The occupied crevices that were fairly close to the ground were always in rocks exposed on extremely steep slopes.

The character of the vegetation limits the choice of roosting sites. Most of the roosts were in semi-arid country that supported low chaparral, the most conspicuous constituents of which were California buckwheat (*Eriogonum fasciculatum*), greasewood (*Adenostoma fasciculatum*), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), and coastal sagebrush (*Artemisia californica*). In these areas the plants were low and did not seriously obstruct the approaches to cliffs and outcrops of rock. In the hills one mile west of Chatsworth, Los Angeles County, however, the chaparral was tall and dense locally, and in this area *Eumops* was not so common as I had expected, probably because tall vegetation encroached on many of the likely-looking crevices and did not allow a clear approach from below.

The crevice shown in figure 2, plate 1, harbored roughly six *Eumops* at the times of most of my visits, and is typical of many roosts found in localities having extensive exposures of granitic rocks. The crevice was in a large boulder of granodiorite situated roughly 100 yards from the base of a chaparral-covered slope three miles northeast of Perris, Riverside County.

On several occasions a roosting place was kept under observation during the early morning hours when *Eumops* was returning from foraging. Without exception the bats entered the roost by swooping up into the entrance from below, grasping the surface of the rock with both the thumbs and hind feet, and crawling up into the crevice. This maneuver is generally executed so rapidly that the bat simply seems to disappear after reaching the mouth of the crevice; this makes the action difficult to analyze. This bat

seems never to cling just inside the entrance of the crevice after alighting, but crawls as rapidly as possible into the inner parts of the retreat. This behavior may be important in keeping the entrance clear when bats are entering the roost in rapid succession. Also, it probably makes the bats less vulnerable to predation when they are entering their roosts.

In its roost *Eumops* crawls forward at varying rates of speed. In merely shifting its position slightly, the animal usually crawls slowly and appears awkward and faltering in its movements, but at other times crawls fairly rapidly, even when moving but short distances. When entering the roost after a night's foraging, or when frightened and forced to move long distances, this bat loses its appearance of awkwardness and can move with remarkable speed. The bat can crawl almost as rapidly within the confines of a narrow crevice as across a level cement floor, and in a crevice is able to maintain forward speed until its dorsum and venter are in contact with the rock surfaces. At this point the bat turns around, and in an upside-down position, wedges itself into the crevice by crawling backward. The hind feet reach behind the animal, grope about, and when a solid foothold is obtained pull the bat backward; the bat pushes with its wings, keeping the thumb and pad at the ventral base of the first metacarpophalangeal joint against the substrate. I have never observed this bat resting in any other position than upside-down, with its body wedged either tightly into a crevice or with the dorsum and venter at least touching the rock. When roosting in buildings *Eumops* seems to behave differently, for Howell (1920a:114) found individuals hanging against the ridge pole of an attic near Covina, Los Angeles County, California.

Eumops moves about in its roost at any hour of the day, but according to my observations is most active in early morning and late afternoon, at which times the bats are fairly vocal. On several occasions a colony was observed in the morning and again in late afternoon. In the morning the bats were invariably in the deeper parts of the crevice, but in the afternoon usually some were at places nearer the entrance. Individual bats roosting alone seem to move relatively little in the daytime.

In some roosts, *Eumops* must crawl fairly long distances from the part of the crevice in which it roosts to the launching place. In large crevices these bats usually crawl far into the deeper recesses to rest, and in several large crevices the bats habitually rested roughly 15 feet from the mouth of the crevice. As the time for the

evening exodus approached, one or two bats at a time moved from the resting place to near the launching place. Usually the bats did not leave the roost in rapid succession, but launched themselves singly, at irregular intervals. On August 20, 1953, in San Diego County, a colony of *Eumops* was observed from 5:30 P.M. until 10:30 P.M. (these and all other times mentioned are Pacific Standard times). The first *Eumops* launched itself at 7:55, and between this time and 10:30 only six more bats left the crevice. At 10:30 one bat was near the mouth of the crevice and four or five were still far back in the crevice. Throughout the period of observation there was much movement within the crevice. On June 21, 1954, at another colony in San Diego County, it took 26 minutes (7:27 P.M. to 7:53 P.M.) for the 19 adult members of the colony to take flight.

The mechanical arrangement of the hind limbs of *Eumops* does not favor quadrupedal locomotion; nevertheless, because of the strength of the musculature of the pectoral girdle, this bat can crawl rapidly for fairly long distances. While the animal is crawling, the body remains parallel to the ground and the ventral surface of the bat is elevated slightly above the substrate. The tail curves upward at an angle to the substrate of roughly 45 degrees and probably serves as a sensory organ when the bat is moving either frontward or backward in a crevice. The head is held low, in line with the body. The limbs are used alternately, as is the case in lizards and most cursorial animals. While the forelimb on one side is at the forwardmost part of its stride the hind limb on the same side is extended to the rear at the end of its propulsion stroke. The limbs on the opposite side of the body are in the reciprocal phase of the cycle.

During quadrupedal locomotion this bat keeps the digits fully flexed and the wing-tip is folded against the medial surfaces of the distal parts of the first and second metacarpals. The elbow and humerus are held fairly close to the body. The calcar is laid back near the posteromedial surface of the shank, and the uropatagium is pulled toward the base of the tail. The proximal part of the posterior edge of the plagiopatagium is pulled upward, out of the way of the hind limb, by the partly flexed forelimb. The long axis of the humerus is roughly parallel to the substrate throughout most of the stride, while the forearm angles downward and the thumb and thumb-pad contact the substrate during the rearward (propulsion) part of the stride. In the course of a stride the forelimb makes a movement that resembles a paddling stroke. The fore-

arm is partly flexed and is directed forward and laterad at the beginning of the propulsion stroke of the stride; the humerus is partially extended at this point in the stride. The propulsion part of the stride is produced by the extension of the forearm and flexion of the humerus, these actions tending to pull the forearm caudad while keeping the carpus roughly the same distance from the body. In the propulsion part of the stride the forearm moves through an arc of some 40 degrees. At the start of the forward part of the stride the forelimb is lifted from the substrate by abduction of the entire limb, and is brought forward by flexion of the forearm and extension of the humerus. This action is extremely rapid; although the photograph of *Eumops* in the midst of the forward part of the stride shown in figure 3, plate 4 was taken at one two-thousandth of a second, the distal half of the forearm is blurred. At the end of the forward part of the stride the forelimb is adducted and the propulsion stroke begins. Because the humerus is directed laterad while the animal crawls, the forelimbs are splayed out to the side. Accordingly, although the movement of the humeroradial joint is anteroposterior, the plane of action of the limb is directed laterad, and is not vertical to the substrate as in cursorial mammals. The long forelimb, therefore, can go through the motions of the stride without markedly increasing the height of the space necessary to allow passage of the animal's body. Because the limb is directed more or less laterad the adductors must act to enable it to bear part of the weight of the body and the abductors must help in the forward part of the stride. Thus, not only are the extensors and flexors of the forelimb brought into play in quadrupedal locomotion, but the adductors and abductors are of considerable importance.

The hind limb of *Eumops* is used in reptilian fashion in quadrupedal locomotion. The long axis of the femur is held more or less parallel to the substrate or angles slightly dorsad from the pelvis, and the shank is vertical to the substrate or, in the propulsion part of the stride, is directed slightly caudad. At the start of the propulsion part of the stride the femur is directed craniolaterad, the shank is extended beyond right angles to the femur, and the foot is roughly in alignment with the long axis of the body. In producing the propulsion part of the stride the femur is pulled caudad; the shank is flexed through the middle part of the stride, and then extended at the end of the propulsion part of the stride, when the femur is directed caudolaterad. When the feet are in contact with the substrate the toes are spread widely apart. The direction

of movement at the hip joint in quadrupedal locomotion, then, is anterior-posterior; the plane of movement extends laterad. The direction of movement at the knee joint is dorsal-ventral; the major plane of movement of the shank in the stride is anterior-posterior. The propulsion is provided mainly by anterior-posterior movements of the femur and by the extension and flexion of the shank. The adductors and abductors of the hind limb are also important, for the former supports the weight of the posterior part of the body and the latter helps in the forward part of the stride.

The limb action used by *Eumops* in crawling seems awkward, but if it is remembered that this bat is primarily a crevice-dweller, its type of locomotion is seen to be remarkably effective. The action of the limbs is directed largely laterad, so that the animal requires little more "headroom" when crawling than when at rest, and can crawl at full speed in a fairly narrow crevice without having the movement of the limbs restricted. Howell (1920a:116) comments that mastiff bats are agile on the ground, and describes the action of the forelimbs in crawling as being "over-hand." Although the bat does sometimes give this impression, high-speed photographs show that movement of the forelimbs is directed mainly laterad, even when the animal is not in a confining space (Pl. 4, Figs. 2, 3).

Foraging Habits and Flight

The spectacular manner in which *Eumops* launches into flight has been described briefly by Howell (1920a:117) and Krutzsch (1955:410). All of my observations of these bats taking flight were made on individuals emerging from crevices in rock. When a group of mastiff bats are roosting together they become increasingly active as darkness approaches. When poised at the mouth of the crevice, shortly before launching into flight, they chatter loudly and emit loud "smacking" noises; as a bat launches itself it gives a series of piercing, high-pitched cries. The bat drops from the mouth of its crevice and dives rapidly downward until sufficient air speed is gained to allow the bat to begin level flight. The wings usually give several powerful strokes as soon as the animal drops clear of the mouth of the crevice, and the bat dives at an angle of roughly 45 degrees for some 10 to 20 feet before it pulls upward in a wide arc and assumes level flight. At a colony three miles east of El Cajon, San Diego County, it was possible to estimate fairly accurately the distance the bats dropped before leveling off. The crevice from which the bats emerged was in a large granite boulder

on the west side of a ridge and was approximately 22 feet above a steep chaparral-covered slope that was dotted with large boulders. The bats habitually dove downward and away from the cliff to about opposite the level of the base of the colony-rock before beginning level flight; thus most of these bats dropped between 20 and 25 feet. At this roost occasional individuals were observed to leave the roost in a different fashion. Instead of leveling off after dropping some 20 feet, these bats cleared the boulder directly beneath the colony-rock by a few powerful wing-beats and then resumed their steep dives; with erratic strokes of the wings and rapid twists and turns they slanted down the slope at high speed, clearing the brush and boulders by some 10 feet. After diving some 100 yards the bats leveled off and circled near the colony-site for a short time before flying off. A female *Eumops* from this colony was launched by hand near the base of the colony-rock in the daytime; she dove rapidly far down the slope and was lost to view. The character of the terrain adjacent to the roosting-site seems to affect the way in which *Eumops* takes flight; bats usually emerged from roosts beneath which there was relatively little space by diving only five or 10 feet and then pulling sharply upward.

Howell (1920a:112) thought that *Eumops* could not take flight unless able to launch itself from a considerable height. Krutzsch (1955:408) agrees that this bat is reluctant to take flight when low to the ground, but he observed an individual to fly across a room 30 feet in length from the top of a laboratory table that was only two and a half feet above the floor, and had another bat fly when dropped from six feet in the air. Individuals that I tested were never able to take off from the ground or from other flat surfaces, and were also unable to maintain flight after launching themselves from the tops of tables. On several occasions, however, I was able to launch mastiff bats into flight by throwing them some 15 feet into the air, whereas bats thrown half this distance did not fly. On one occasion a male *Eumops,* which I had recently captured, was able to take flight from a granite bench with roughly a 20 degree slope. Judging from my experience with *Eumops,* and from the published observations of others, this bat is totally unable to take flight from a level surface. Probably five or six feet from the ground represents the minimum height from which the bat can launch into sustained flight.

Eumops emits a single high-pitched, piercing cry of short duration, which can perhaps best be described as a staccato "chip,"

every two or three seconds as it flies high above the ground, away from obstacles. The intervals between the cries are not always constant, and as the bat approaches the ground the intervals decrease, until as the bat nears some obstacle or makes its approach to the roosting-crevice the cries no longer are separate but blend together in a high buzz.

Characteristically this bat forages at a considerable elevation. Most of my estimates of the height at which *Eumops* flies are the result of inference, but on several occasions, just at dusk, this bat was watched with binoculars as it gained altitude and flew out of sight above the colony. At a deserted granite quarry six miles west of Riverside, Riverside County, on the night of July 9, 1954, from a vantage point on the west slope of a ridge above the quarry, I watched two *Eumops* leave their roosts while it was still fairly light. The first bat emerged at 7:42 P. M., flew over the floor of the canyon below the roost, and climbed in large circles out of sight to the northwest. This bat was watched partly with the aid of binoculars and was an estimated 1000 feet overhead when lost to view. For some time after it could no longer be seen this bat's strident cries could still be heard. Another *Eumops* took flight at about 7:50 P. M. and was watched briefly as it circled upward. On this evening it seemed that the cries these bats made could be heard clearly when the animals were some 1000 feet overhead. At another colony a bat under observation disappeared from view when an estimated 800 feet away, but its cries could still be heard a short time thereafter.

Indirect evidence also indicated that *Eumops* forages, or at least habitually flies, high above the ground. On the basis of the above observations, it seems that the cry emitted by these bats as they fly can be heard clearly at a distance of approximately 1000 feet. Therefore, when these bats are heard at night directly overhead a rough estimate can be made of their distance above the observer by taking into account the faintness or loudness of the cries. These estimates are admittedly not accurate, and must be influenced strongly by the differences in the acoustical characteristics of the air from evening to evening (Knudsen, 1931, 1935), but this is the only method I found for estimating the height at which *Eumops* flies in the hours of darkness.

While watching roosting sites of *Eumops* at night, I often heard these bats fly nearby, and many opportunities to gain a general idea of the height at which they fly were thereby afforded. At the

colony near El Cajon, San Diego County, I repeatedly heard individual bats or small groups pass over the colony-site at such an elevation that their cries were barely heard. *Eumops* was commonly heard also as it flew immediately above the colony-site, but rarely was it heard below the site. At this same colony, on an evening when high fog enveloped the area by about 9:00 P. M., few *Eumops* were heard and those that did fly over were near the limit of audibility. These bats may have been as much as 2000 feet overhead and more than 3000 feet above most of the surrounding countryside. In August of 1954 several roosts in Los Angeles County were observed periodically, and bats in this area were also heard at night, many times high above their colony-sites. From a cliff that faced north from the crest of the eastern end of the Santa Monica Mountains, Los Angeles County, on a summer night when fog covered the lowlands by early evening and pushed up the slopes of the mountains to the level of the crest by shortly after midnight, I heard groups of *Eumops* far overhead, their cries sounding distant and faint; occasionally small groups flew close to the cliff. Although it often flies extremely high, this bat may regularly be heard as it flies only 100 to 200 feet from the ground. Over the coastal parts of San Diego County, and over the valleys of San Bernardino and Riverside Counties *Eumops* seemed to fly commonly within several hundred feet of the ground. At Hetch Hetchy Dam, Tuolumne County, in the summer of 1952, these bats were heard many evenings as they flew within 100 to 200 feet of the surface of the water. There, observations were made from a granite bench that rose high above the water, and estimates of the elevations at which the bats flew were fairly accurate because the height of the observer above the water was known.

Both the character of the terrain and the weather conditions probably influence the elevation at which these bats forage. Over broken country they seem to fly higher than over level sections. On foggy nights, in several localities in southern California, I was impressed by the apparent absence of mastiff bats during part of the night and their return to the roosts in the morning. Possibly this bat flies high, or flies many miles away from the colony-site, to avoid weather unfavorable for successful foraging. The nocturnal presence of *Eumops* on the western borders of the Mojave Desert of California seems to be sporadic, and the bat's occurrence in this area conceivably is governed by weather in adjacent coastal areas. On many nights in August and September of 1954, on the

Mojave Desert six miles west and one mile north of Lucerne Valley, San Bernardino County, small groups of mastiff bats repeatedly were heard overhead starting at roughly 10:00 P. M., whereas on other nights the bats seemingly were not present in the area. It was not determined whether or not their presence was correlated with the occurrence of fog in the nearby coastal sections. Bad weather as such, however, does not seem to keep *Eumops* from flying. Individuals have been heard on rainy nights in the vicinity of Claremont, Los Angeles County. In the early morning of July 13, 1954, at the colony site near Perris, Riverside County, a violent thunderstorm lasted roughly two hours; many times in the storm mastiff bats were heard overhead.

On the basis of much indirect evidence, the foraging range of *Eumops* seems to be extensive. On numerous occasions, late at night, these bats have been heard flying over areas supporting continuous tracts of chaparral, or over level desert flats five to ten miles from the nearest places that a mastiff bat could roost. Groups of these bats that were heard at various localities on the Mojave Desert of western San Bernardino County were probably no less than 15 miles from their roosts. In these instances searches for colonies of *Eumops* in the closest desert hills always failed to produce evidence of the bat's presence, and their cries never indicated that they were leaving roosts in these hills in the evening. Almost without exception the direction of the first cries of mastiff bats that were heard in the evening in this area suggested that the bats were coming from the west, from the coastal sections. Although localities that provide suitable roosting sites for *Eumops* are by no means of continuous occurrence in southern California, these bats are, as indicated by their cries, widespread late at night, occurring from the seacoast to the western parts of the deserts. From the above kinds of evidence, I conclude that *Eumops* generally has a nightly foraging radius of at least five miles, and that these bats may forage regularly as far as 15 miles or more from their roosts.

The flight of this bat is strong and fast. Because of its late emergence this bat can seldom be seen in flight except at close range by moonlight or by flashlight. Most of my observations of *Eumops* in flight were made of bats emerging from their roosts or of individuals released in daylight. The flight is more direct and less erratic than that of most other bats; the wing-beats appear to be slower, and, at least in level flight, shallower. On a still evening the sharp swishing of the wings can be heard up to a distance of

roughly 100 feet. Using the sound of the wing-beat as these bats flew by colony-sites as a guide, I estimated on several occasions that there were approximately four beats per second in level flight. During sudden turns, or when climbing rapidly, the wings appear to beat much faster than this rate. Often, when diving, the wings are held partly closed and rigid. When diving rapidly down a slope after emerging from its roost *Eumops* looks somewhat like a large, heavy-bodied swift. In level flight it resembles a medium-sized charadriid shore bird.

Often, late at night and early in the morning, mastiff bats dive repeatedly past a colony-site. This behavior was noted at three different localities and the maneuver is illustrative of some of the aerial capabilities of this bat. These dives are always heralded by a sudden increase in the rate of the cries given by a passing *Eumops*. Then, with the cries merged into a continuous buzz, the bat dives at high speed toward a point below the roosting-crevice, pulls sharply upward just before reaching the cliff, and performs a half loop which takes the animal out away from the cliff and well above the level of the roosting-crevice. The dive is usually made at an angle of at least 25 degrees and at the start of the dive, in a manner reminiscent of the beginning of a falcon's stoop, the wings give several powerful strokes to send the bat slanting rapidly downward on partly closed wings. At the bottom of the dive the wings are spread suddenly, and as the bat pulls up and away from the cliff, the wing membranes produce a penetrating swishing sound like canvas being lashed through the air. The wing strokes resume at the top of the half loop and the sounds they make then recede into the distance. A bat may dive repeatedly at the cliff and then leave the vicinity of the roost; or after several dives a bat occasionally enters the crevice. On one evening at the colony three miles east of El Cajon, San Diego County, a bat made more than 20 dives at the colony rock before flying off. This "buzzing" of the colony-site is not always done in the same way. Sometimes the bats approach the cliff from the side and instead of swooping upward at the last minute simply turn sharply away from the cliff and slant upward at a shallow angle. During their dives the bats are traveling at a speed that appears to me to be comparable to that of a stooping sparrow hawk (*Falco sparverius*), yet the bats are able to turn abruptly upward at the last instant and avoid the cliff. This suggests the flight of mastiff bats is fairly maneuverable despite its speed.

When alighting at the mouth of the crevice *Eumops* makes a dive that resembles that described above. In fact, when the diving behavior was first observed, I assumed that the bats had to dive at the cliff several times in order to judge their landings properly. Early in the morning, when bats are returning to the roost, however, they generally enter the crevice on the first dive, while bats usually leave the vicinity of the roost after making many dives. The dive executed immediately before alighting seems to be made at a fairly shallow angle. The bat dives for a point some 10 or 15 feet below the roost-entrance, then swoops upward just short of the cliff and seems literally to fly into the crevice. Close observation indicates that the bats are nearly at the stalling point when they reach the mouth of the crevice, but have enough momentum to help them scramble rapidly into the deep part of the crevice. I have never seen *Eumops* alight in any other way. Members of a large colony of Brazilian free-tailed bats (*Tadarida brasiliensis*) at the eastern end of the Santa Monica Mountains, Los Angeles County, entered a hole in a cliff after a maneuver that resembled that employed by *Eumops*. The choice of a roosting site by *Eumops* may be determined as much by this bat's need for space to allow it to swoop upward and alight as it is by the animal's need for adequate launching space.

Mastiff bats have a long foraging period. Howell (1920a:117) stated that these bats have a pre-midnight foraging period that lasts roughly 45 minutes, but Krutzsch (1955:411) concluded from his experience with this bat that *Eumops* does not return to its roost until some time after midnight. I have maintained a number of all-night vigils at or near four roosting-sites of *Eumops*, and my observations indicate that this bat usually flies continuously from shortly after dark until early in the morning. Krutzsch (*loc. cit.*) suggests that *Eumops* practices night-resting, as do many other bats, but to me, this seems unlikely for two reasons. One is that mastiff bats require a special type of roost that is not of common occurrence, and although many roosts known to be occupied during the daytime were visited at various times of the night, *Eumops* was seldom observed to return to a roost to rest. The longest time a bat remained at the roost after returning at night was less than half an hour. Secondly, it is usually possible to hear the cries of flying *Eumops* in every hour of the night in suitable areas; rarely does there seem to be a time of peak activity and then complete absence (except occasionally on foggy nights).

The time of emergence varies, but is characteristically at dark, roughly one hour after sunset. Generally these bats begin leaving their roosts 40 to 50 minutes after sundown, but many leave later, from roughly one hour to one and one-half hours after sunset. By one and one-half hours after sunset most mastiff bats have left their daytime retreats. In the summer of 1954 the time of the first emergence of *Eumops* in the evening varied from 40 minutes to one hour and five minutes after sundown. On one evening a colony was watched for more than two and one-half hours after sunset and although seven bats left the colony several adult bats still were in the crevice.

Mastiff bats return to their roosts early in the morning. The occasional individuals that return to the crevice in the night and stay for a short time are usually females with young in the roost. In midsummer small groups of *Eumops* generally begin returning to the immediate vicinity of the colony-site about 2:00 A. M., two and one-half hours before sunrise. The groups circle around the area and bats periodically dive near the crevice; often after staying near the roost for a few minutes the group will leave the immediate area. The first bats generally enter the crevice shortly after 2:00 A. M. Aerial bat activity near the colony-site usually reaches its peak sometime between 2:30 and 3:00 A. M., and most of the bats enter the roost in this period. In the summer of 1954 the earliest time at which a colony began entering its roost was approximately 2:00 A. M., two and one-half hours before sunrise, and the latest arrival recorded was at 4:06 A. M., 45 minutes before sunrise. The following are excerpts from notes taken on June 20, 1954, at the colony three miles east of El Cajon, San Diego County; they give an idea of the pattern of nocturnal activity at a *Eumops* colony.

6:00 P. M. Bats chattering and chirping, noise continuing nearly uninterruptedly.

7:25 P. M. Loud "smacking" noises at mouth of crevice and much movement in crevice.

7:30 P. M. Two bats left roost; they dove down steep slope below colony-rock, leveled off and flew nearby for a short time.

7:45 P. M. Nine bats have left crevice; some dropped from crevice and flew out from rock in shallow arc, others dove down slope.

7:50 P. M. One bat left crevice.

7:55 P. M. Roughly six or eight bats left since 7:50; all bats (except several young far back in crevice) have emerged.

8:12 P. M. Two or three bats swooping past crevice; bats left area after five minutes.

8:30 P. M. Several bats back flying over colony-rock.

8:45 P. M. One bat swooped by crevice several times, then entered crevice.

8:50 P. M. Bat that just entered crevice (8:45) left crevice.
9:55 P. M. Two bats back diving past crevice, then left area.
10:00 P. M. Two bats entered crevice after several preliminary swoops.
10:15 P. M. One bat swooped by crevice more than 20 times, then left.
10:25 P. M. Two bats (that entered crevice at 10:00) left.
10:45 P. M. Small group of bats circling rock; one swooped by crevice several times. Group left after five minutes.
10:55 P. M. Group of bats flying overhead.
11:20 P. M. Single bat flying near rock; made 16 dives but did not alight; left in few minutes.
1:10 A. M. Between 11:20 P. M. and 1:10 A. M. several groups of bats came near colony-rock and dove by crevice.
2:00 A. M. Several bats swooped repeatedly by crevice.
2:05 A. M. Two bats entered crevice.
2:15 A. M. Large group of bats circling around rock; individuals occasionally diving by rock.
2:17 A. M. One bat entered crevice.
2:20 A. M. No flying bats within hearing.
2:25 A. M. Group of bats near rock; several swooping by crevice.
2:27 A. M. One bat entered crevice.
2:28 A. M. Two bats entered crevice.
2:35 A. M. One bat entered crevice.
2:40 A. M. Group flying high nearby (have been overhead since 2:25).
3:31 A. M. Between 2:45 and 3:30 twelve bats entered crevice.
4:00 A. M. Sky fairly light; seemingly all bats back in crevice; much amiable squeaking.

On the basis of the above and many similar observations I conclude that in the summer *Eumops* has a single, long, foraging period per night. This period seems to vary from night to night and between individual bats on a given night. Generally the foraging period is roughly six and one-half hours in length, and throughout this time most *Eumops* fly continuously. For bats, this is an unusually long foraging period, and indicates that mastiff bats are not only fast, but enduring fliers.

Eumops is insectivorous. Droppings invariably consist of small fragments of insects. This bat normally forages between several hundred and 2000 feet above the ground, and the question arises as to what insects occur at these levels, and how these insects get there. Insects are not known to fly regularly at such elevations, but little is known of this aspect of insect ecology. It is known, however, that during the daytime rising masses of air take insects up the slopes of mountain ranges or lift insects high above the surface of the ground. Many of the areas inhabited by mastiff bats are fairly hot in the summer and are characterized by surface topography of high relief; such areas promote turbulence of the air, and the thermals and convection currents produced in the day-

time probably carry many insects high above the ground and well away from their normal habitats. How long insects carried by air currents to high elevations stay at these levels has not been determined, but it is possible that considerable numbers remain throughout the night at the elevations at which *Eumops* usually forages. Because it has a wide foraging range and is a speedy flier, this bat could probably catch an adequate number of insects even if the insects were far less numerous within the elevational belt at which this bat forages than they are close to the ground. Temperature inversions are prevalent in the parts of California inhabited by *Eumops*. Thus, when mastiff bats forage above a dense low-lying fog on a summer night they are often in considerably warmer air than that near the ground. Possibly some insects tend to concentrate in this warmer air. In southern California on cool winter nights these bats are sometimes heard flying high overhead. On these occasions, due to the temperature inversion that often prevails for many nights in this region, the bats may be in air warmer than that surrounding the observer at ground level. It cannot be said that the bat finds insects, but the fact that these bats fly on such nights suggests that they are feeding.

Myotis velifer

Roosting Habits and Terrestrial Locomotion

Field studies on the cave myotis were carried out chiefly in the vicinity of the Riverside Mountains of Riverside and San Bernardino Counties of southeastern California. The main axis of the range extends from roughly 30 miles to 37 miles north of Blythe, Riverside County. The colonies of bats studied were in mine tunnels in the sides of several large canyons that cut deeply into the eastern slope of the range. Many of the tunnels were part of the old "Mountaineer" mining operation, now bearing the name "New-era Mine." The Riverside Mountains rise approximately 1500 feet above the surrounding arid desert.

Myotis velifer roosts in a variety of situations; its roosting habits have been well described by Twente (1955). In my study area the daytime roosts were all in deserted mine tunnels. Stager (1939:226) found this bat to be absent from this region in the winter and early spring. I found these bats in clusters of from several to more than one hundred individuals in crevices, drill holes and irregular or hollowed-out areas on the ceilings. Each of several tunnels contained roughly 1000 cave myotis, and each of other tunnels was

inhabited by several hundred individuals. These bats usually were most abundant in the deeper parts of the tunnels, beyond roughly 60 feet from the mouth, where they tended to occur in clusters on the ceilings; in the shallower parts of the tunnels the bats generally roosted in crevices or holes, and seldom were found less than 25 feet from the mouth of the tunnel. This species has a strong tendency to cluster, and individuals seem to be ill at ease when apart from others of the species. On several occasions, when I was photographing the flight of *M. velifer* in a deserted cabin, four or five of these bats were observed to alight near one another and immediately cluster together in a tight mass.

This clustering behavior of the cave myotis is thought by Twente (1955) to be associated with temperature regulation both when the bats are active and when they are hibernating; the clustering habit may also enable groups of these bats to exploit roosting sites that cannot be used by single individuals. Considering resting animals, the posture of the hind limbs of *M. velifer* is different from that of the hind limbs of *Macrotus*. The latter is adapted to hanging free from the ceilings of caves; when it hangs pendant the hind limbs and feet are relaxed and project straight behind the animal. The structure of the tarsus and the lengths of the flexor and extensor tendons of the shank are such that the foot is extended, even when relaxed, and thus the foot can retain a grip on some irregularity in the surface of the ceiling when the bat is relaxed or even torpid. *Myotis velifer*, in contrast, normally roosts with its ventral surface resting against something; the hind limbs remain partly flexed with the femur projecting craniolaterad and more or less dorsad and the shanks project posteroventrad and usually slightly mediad. If *M. velifer* were to hang supported by its feet only, the long axis of the body would assume an angle to the ceiling of more than 90 degrees. When relaxed the feet are not extended. Were the bat to hang pendant, the hind limbs and feet would be unable to relax and still maintain a grip on the ceiling. If the body is held in a position somewhere between horizontal and vertical, with the ventral surface and head downward, the hind limbs and feet are able to relax and still cling to the substrate. When forced to hang alone from a sloping ceiling *M. velifer* generally attempts to help support its body by pressing the wings against the slanting surface. I have never seen this bat hang singly from a ceiling, and Stager (1939:227) states that he has never seen a myotis of any species hang from a ceiling by its claws only. Seem-

ingly, because all the members of a cluster of bats have their ventral surfaces in contact with other bats or some other supporting surface, their bodies are held in such positions that the hind limbs and feet may relax and still maintain a grip. This attempt to keep the ventral surface in contact with a supporting surface may be one reason why peripheral members of a cluster of bats always have their bellies facing toward the middle of the cluster.

In their usual daily cycle of activity, when roosting during the daytime in a cave or mine tunnel, these bats seem to use quadrupedal locomotion but little. They move over the rock walls of a cave only occasionally to seek better roosting sites and crawl short distances within a roosting crevice. I have never seen *M. velifer* crawl long distances under natural conditions.

Despite the seeming unimportance of quadrupedal locomotion in this species, it is able to crawl and climb fairly well by using its forelimbs and hind limbs in approximately the same fashion as that described for *Eumops*. When crawling, *M. velifer* raises the anterior part of the body farther off the substrate than the posterior part of the body, and the tail is curled ventrad and forward. When in contact with the substrate, the forearms incline ventrad more than do those of *Eumops*. When the animals are crawling, the body of *M. velifer* is at a considerable angle to the substrate, whereas that of *Eumops* is almost parallel to the substrate. This same difference has been noted by Orr (1954:200) between the postures of crawling *Antrozous pallidus* and *Tadarida brasiliensis,* and may be a consistent difference between the family Vespertilionidae and the family Molossidae. Judging from the literature and from my own observations, vespertilionid bats crawl less rapidly than molossid bats, probably owing to the lack of freedom of the hind limbs from the flight membranes and the relatively shorter, less rapid strides of the forelimbs in vespertilionid bats. The uropatagium in most vespertilionids is large, and incapable of sliding proximad along the caudal vertebrae, and leaves less of the tail free than in molossids in which the tail is mostly free when the bat crawls. In vespertilionids, accordingly, the hind limbs are not able to move so freely during terrestrial locomotion as do those of molossids. Assuming that *M. velifer* and *E. perotis* possess the types of quadrupedal locomotion characteristic of the family Vespertilionidae and Molossidae respectively, the posture of the forelimbs of vespertilionids is probably more efficient in terms of energy necessary for the stride because the limbs are oriented more nearly vertically to the substrate than the ventrolaterally directed forelimbs of molos-

sids. Because of the slightly upright posture of the body and the partially vertical action of the forelimbs, however, quadrupedal locomotion in vespertilionids is not so efficient within the confines of a narrow crevice, where, judging from my observations on *E. perotis, Tadarida molossa* and *T. brasiliensis,* the locomotion of molossid bats is remarkably effective.

Foraging Habits and Flight

Cave myotis take flight and alight in the manner common to most vespertilionids. When launching itself *M. velifer* drops from its roosting place with its wings partly open, spreads its wings and starts beating them rapidly when clear of obstructions, and pulls upward into level flight at from a few inches to a foot or two beneath the roosting place. These bats can easily launch into flight from a level surface by pushing off with their wings and feet. Landings are usually made on steeply sloping ceilings or vertical surfaces, and the landing surface is grasped with the thumbs and hind feet. The landing is made with the head upward. The uropatagium is lowered and spread just before the landing and the wings are fully spread; the bat slows down rapidly and when near the stalling point comes into contact with the landing surface roughly simultaneously with both the forelimbs and the hind limbs. When a solid foothold is gained the bat releases its hold with the thumbs and one foot and moves into a head-downward position. Often, instead of finding a foothold and assuming a head-downward position immediately, the bat feels about with its feet while bracing its body with its forelimbs, and slowly shifts into the head-downward position.

The flight of the cave myotis is stronger and more direct than that of most members of the genus *Myotis,* but is highly maneuverable. On many evenings when western pipistrelles (*Pipistrellus hesperus*), California myotis (*Myotis californicus*) and *M. velifer* were foraging at the same time over common ground, the more rapid, less fluttery flight of *M. velifer* was accentuated by the erratic flight of the smaller species. When foraging this species flies fairly steadily until an insect is perceived, then the flight often becomes extremely erratic. After the insect is captured the bat continues on its relatively straight course until another insect is chased. The foraging flight of the cave myotis thus alternates between direct, steady flight, and abrupt twists and turns. When sudden changes of direction are made the uropatagium and wings are normally spread fully, and the bat uses the full area of its flight membranes

as a braking surface. From level flight these bats turn upward, downward, or to the sides to chase insects, but seem not to chase their prey upward as often as in the other directions. The pinnae of *M. velifer* face forward and slightly downward and to the side when the animal is in flight; insects are perhaps perceived more often when they are in front, below, or to the sides of the bat than when they are flying above the bat. Hall and Benson, while observing bats in Nevada (Hall, 1946:142), noted a positive correlation between the directions in which the pinnae of the different species faced and the directions in which insects were pursued. In the Riverside Mountains area, after leaving their daytime retreats, cave myotis usually flew directly down the eastern slope of the range to the floodplain of the Colorado River where they foraged. The flight at such times was steady and fairly rapid, and when flying down steep slopes the bats occasionally partially closed their wings, dived rapidly, and skimmed not over five feet above the large creosote bushes and jutting outcrops of rock. On the other hand, when this bat is in a cave or mine, or other restricted area, it travels more slowly and the wing-beat is shallower and seems more rapid.

In the Riverside Mountains area these bats forage mostly over the floodplain of the Colorado River, where they pursue foraging beats over low vegetation, along the files of dense vegetation that line the oxbows and main channel of the river, between the scattered thick patches of vegetation that dot the floodplain, or above bodies of water. The dense linear stands of screw bean (*Prosopsis pubescens*), tamarisk (*Tamarix*), catclaw (*Acacia Greggii*) and mesquite (*Prosopsis* sp.) that border the still water of the oxbow ponds seem to constitute optimal foraging habitat, and in such localities just before dark on a summer evening there are usually six or eight *M. velifer* in view at all times. These bats do most of their foraging between roughly six and 15 feet of the ground, and prefer to forage close to vegetation. When foraging near large patches of vegetation these bats often fly within a few inches of the foliage; in chasing insects the bats often fly through small spaces between branches or through narrow corridors between adjacent plants. Under some circumstances, these bats flew back and forth over definite foraging beats estimated to be from 50 to 70 yards in length.

The character of the vegetation affects the mode of foraging of *M. velifer*; near mesquite or tamarisk, or other plants that normally grow to at least nine to 12 feet in height, this bat flies near the plants, and stays six to 12 feet from the ground, usually keeping to

the level of the main mass of foliage rather than foraging above it. Near patches of arrow weed (*Pluchea sericea*), the bat forages mostly five to eight feet above the ground, just above the vegetation. While chasing insects under these conditions these bats sometimes fly through spaces between the wandlike arrow weeds and descend to within three or four feet of the ground. Also, when foraging over low cattails (*Typha* sp.) or open water this bat is apt to fly lower than it does around tall vegetation. Although seemingly not so common in these areas, *M. velifer* often forages over dry washes where it tends to fly from ten to 15 feet above the ground, at the level of the thickest parts of the larger mesquite, catclaw and palo verde (*Cercidium floridum*). In open desert, dominated by the creosote bush (*Larrea divaricata*), where I have observed this bat foraging on relatively few occasions, it flew just above the level of the bushes, four to seven feet above the ground. Within the general elevational zone at which *M. velifer* forages, then, it usually flies close to foliage, and the shapes of the plants and the level at which the densest vegetation occurs seems to govern the elevation at which the bat flies.

In the evening *M. velifer* usually emerges from its daytime roost well before dark, and for a short period forages with, but at a lower elevation than, the western pipistrelle. In June of 1953, the times of emergence of these bats from their daytime retreats varied from 7:08 P. M. to 7:50 P. M. (17 minutes to one hour and four minutes after sunset), and the average time of emergence was 37 minutes after sunset. In late June of 1954, these bats emerged somewhat later, appearing at from 42 to 55 minutes after sunset. The temperature was higher in late June of 1954 than in early June of 1953, and may have affected the time of emergence of the bats. I gained the impression that this species started foraging later on hot nights than on cooler nights. All of the individuals of a colony of cave myotis do not leave their daytime roost together in the evening. As an example, at a mine tunnel in the Riverside Mountains, on June 6, 1953, it took 47 minutes for the emergence of a colony of roughly 200 of these bats. To an observer stationed on their foraging grounds, however, this species seems to appear suddenly in large numbers. Twente (1955) gave a good description of the emergence of large colonies of *M. velifer* from caverns in south-central Kansas.

The pre-midnight foraging period of this bat lasts until nearly midnight. Individuals with full stomachs have been caught enter-

ing night-roosting places at from 8:10 P. M. to 11:41 P. M. (one hour and 22 minutes to four hours and 53 minutes after sunset). Each bat probably forages for considerably less than an hour in this period; individuals captured near midnight probably were moving from one roost to another or were doing a limited amount of foraging after their main foraging period. Almost without exception, cave myotis that were obtained after 8:15 P. M. (one hour and 27 minutes after sunset) had full stomachs. Considerable evidence suggests that in summer *M. velifer* fills its stomach within roughly one-half hour after emerging in the evening. For example, on August 22, 1957, two individuals were shot as they foraged over an oxbow of the Colorado River 57 minutes after sunset and roughly 30 minutes after the first *M. velifer* was seen foraging on that evening; the stomach of one bat was nearly full, and that of the other was slightly more than half full. As evidenced by sight records of foraging cave myotis and tabulations of numbers of individuals entering night-roosting places, the greatest nocturnal activity of these bats occurs between 35 minutes after sunset and four and one-half hours after sunset.

In the middle of the night these bats roost in some sheltered place and rest; there seems to be no clearly defined second foraging period in early morning. This species has been observed night-roosting in a variety of buildings, caves and mine tunnels. When night-roosting these bats are more likely to roost singly or in small groups than they are in the daytime. Night-roosting has been observed in every hour between one and one-half hours after sunset and one and one-half hours before sunrise, and the bats have been recorded returning to their daytime roosts between 1:30 A. M. and 3:30 A.M. (roughly three hours to one hour before sunrise). The records of cave bats taken at the entrances of daytime and nighttime roosts in early morning hours indicate that there is no long or well defined early morning foraging period, and that the bats do not attempt to fill their stomachs just before daybreak; in fact *M. velifer* often goes to roost for the day with an empty or only partially full stomach. Many specimens were taken at their daytime roosts immediately after sunrise, and the stomachs of most of them were either empty or only partially full. Between June 6 and 15, 1953, 15 cave myotis were taken as they entered roosts between 12:50 A. M. and 3:28 A.M.; the stomach of none of these bats was more than half full, and most of the stomachs were one-quarter full or less. From evidence of this sort, I conclude that

these bats rest during most of the early morning hours, and that there is no regular foraging period after midnight, but that many individuals do a limited amount of foraging between midnight and sunrise. It further seems likely that counting the time necessary for the bats to travel from their daytime roosts to their foraging areas and back *M. velifer* is on the wing no more than one and one-half hours per night.

My field studies have given little basis for a general knowledge of the foraging range of this species. In two localities foraging areas of these bats were slightly more than a mile from the nearest roosts. *M. velifer* is a strong flier, and I expect its nightly foraging range under some circumstances is more than this distance.

Macrotus californicus

Roosting Habits and Terrestrial Locomotion

Macrotus was studied in the field mainly in the Riverside Mountains of California, in the same localities at which *Myotis velifer* was studied.

In the study area *Macrotus* roosts in the daytime exclusively in caves, deserted mine tunnels and deep grottos. In the Riverside Mountains many of the deserted mine tunnels in the steep sides of the rocky canyons were inhabited by groups of from several to 100 or more of these bats. They usually were within 30 to 80 feet of the entrance of a tunnel, and seemed not to require dark retreats. On many occasions leaf-nosed bats roosted in short tunnels less than 20 feet deep and fairly brightly lit. Small groups of these bats roosted in some of the deeper natural grottos in the walls of canyons.

In order to be suitable for occupancy by *Macrotus* a retreat must be mostly inclosed and have overhead protection from the weather. Although this bat is perfectly capable of flying in limited spaces and has been observed on many occasions to fly through a small opening to enter a mine shaft, occupied roosting chambers are usually large enough to provide considerable ceiling surface and flying space. Most of the tunnels inhabited by *Macrotus* were from five to seven feet high and roughly the same width, and were from 15 to more than 100 feet deep. One grotto was inhabited by approximately 15 *Macrotus;* the entrance was roughly 12 feet high and 25 feet wide, and the chamber extended some 30 feet into the side of the canyon. This bat may prefer a large roosting chamber because it provides adequate space for flying when the animal is searching for a suitable place to hang. Another factor governing

the choice of roosts may be temperature, for most of the occupied roosts were fairly cool in summer. For example, on August 15, 1953, a small group of *Macrotus* was hanging in a temperature of 84° F. 45 feet inside a tunnel in the south-facing slope of a narrow canyon in the Riverside Mountains, whereas the temperature outside the tunnel was slightly above 110° F. in the shade. Approximately the same differences in temperatures prevailed at all other roosts at which temperature records were kept.

This bat always rests by hanging pendant, by means of one or both feet, from the ceiling of its roosting place. The wings are loosely folded. Although these bats often roost together in small groups, their bodies usually do not touch each other, and the bats become restless when their bodies are in contact with other bats. They prefer to hang from rough or sloping parts of the ceiling where the irregularity of the surface of the rock enables them to find a solid foothold with a minimum of effort. While settling itself immediately after having alighted, when adjusting its foothold, or when steadying its body in preparation to launching into flight, the ventral surfaces of this bat's feet usually face ventrad and slightly mediad and appear to be actively gripping the rock. At such times the hind limbs may be partly flexed, thus pulling the body toward the ceiling, and the head is often raised while the bat looks about. When *Macrotus* is relaxed the hind limbs are straight, the soles of the feet face ventrad, and the head is pointed downward. This bat seems to rest much of the time while hanging onto the rock with only one foot; the other foot and leg are relaxed and dangle, partly flexed, down to the side of the animal. The free foot is often used for scratching and for grooming the fur, and when the bat is engaged in these activities the body usually swings gently like an erratically disturbed pendulum.

Although it is apparent that *Macrotus* actively grips the surface of a ceiling at certain times, the feet seem able to retain their hold on a rough surface when they are completely relaxed. The strongly recurved claws gain purchase on small irregularities in the rock and help prevent the relaxed foot from loosing its grip; as an added help, the force of the tonus of the muscles of the shank and the build of the tarsus tend to extend the foot slightly when the limb is relaxed, thus pressing the digits against the surface of the rock. Because of the large size of the hamstring group of muscles and the mechanical advantage afforded by their attachments, under the control of the tonus of the hind limb musculature the shank flexes when the hind limb is relaxed.

Macrotus seems unable to perform any type of quadrupedal locomotion. I have tried many times to force this bat to crawl, but always without success. If its wings are free, the bat always launches into flight immediately by pushing off with the wings. The structure of the hind limbs is such that an effective stride can not be accomplished unless the bat is hanging. This bat occasionally "walks" bipedally. The animal releases its hold on the ceiling with one foot, the body swings forward (dorsad in relation to the animal's body) and the free foot flexes, reaches dorsad, and gains a new hold on the ceiling. The other foot then lets go and the body swings forward again at the start of a new stride. In this fashion the bat progresses across a ceiling by a series of short strides of the hind limbs, assisted by the swinging of the body. The plane in which the body swings is roughly parallel with the direction of movement, and the dorsal surface of the body faces the direction in which the bat is moving. The head is lifted dorsad while the animal is moving, and the bat seems to be looking about. Although this is a peculiar-looking type of locomotion, it is fairly rapid, and by it *Macrotus* can travel a foot or two in a few seconds. I have never seen *Macrotus* under natural conditions move more than two and one-half feet at one time by "walking." This bipedal locomotion seems to be used when a bat is seeking a more suitable roosting place, but this type of locomotion seems to be used for this purpose less often than is flight.

On several occasions groups of 20 to 30 individuals were observed for periods of one to two hours in mid-afternoon. If the observer remained still the bats seemed not to be disturbed. Even so, colonies are restless. When alert the bat holds its head up with the occiput against the anterior part of the interscapular area and the large eyes look about. In the daytime, there is much shuffling of wings and adjusting of feet. Often one bat will make a flight of several feet and alight amid several bats hanging close together, whereupon the group of bats will become active and in a few seconds all of the members of the group will be in flight. Usually they assemble in small groups at various places on the ceiling of a roosting chamber; the members of a group usually stay far enough apart so that their bodies are not in contact with each other.

Foraging Habits and Flight

The flight of *Macrotus* is remarkable chiefly for its extreme maneuverability. This bat flies fairly rapidly on occasion, but the usual foraging flight is slow and buoyant, and more nearly silent than that of most bats. While watching bats at the entrances of

caves at night I was able to identify several of the most common species by the sounds of their wing-beats. In level flight the wings of *Macrotus* make a soft fluttering sound that is less sharp and carrying than the sounds made by the wing-beats of most bats.

The method of landing was first mentioned by Howell (1920b: 172) and later by Hatfield (1937:97), but has not been described in detail. High-speed photographs show that the alighting maneuver is remarkably intricate. The bat usually makes a level approach to the intended roosting place. At a point some six to eight inches below the ceiling the wings make a deep downstroke that is directed nearly straight forward, and the hind limbs and uropatagium are lowered. These movements cause the bat to swoop sharply upward toward the ceiling. As the bat nears the ceiling the wings are pulled back in an upstroke while the bat rolls over 180 degrees so that its back is facing downward and the long legs reach for the ceiling. At the peak of the upstroke of the wings the feet are pulled far ventrad and come in contact with the ceiling while the body is almost upside-down with the head downward. After the feet grasp the ceiling the wings make a last downstroke that steadies the body and cushions the impact of landing. Stated briefly, then, the alighting maneuver consists of an upward swoop and a half-roll, at the end of which the feet swing rapidly toward the ceiling, seize it, and the wings give a final beat to steady the bat. Usually no parts of the animal but the feet touch the ceiling when the bat alights, but sometimes the wings touch the ceiling when they are adducted rapidly after the feet have clutched the ceiling. The ears are erect and the head faces toward the intended landing point during the entire maneuver. Often these landings must require remarkably precise judgement of speed and distance, as many landings are made in the midst of a fairly closely-spaced group of bats. It is not necessary for these bats to approach the ceiling rapidly in preparation for alighting; they perform the same landing maneuver after hovering close to a ceiling for several seconds. This half-roll method of alighting was the only one *Macrotus* was observed to use.

Macrotus has two main methods of launching into flight, by dropping from the ceiling and taking flight after a short downward swoop, and by taking flight directly from the roosting place. The first type usually is used when an individual launches itself from a group of bats that are close together, and enables the bat to avoid bumping its neighbors. The bat releases its grip on the ceiling by flexing the hind limbs and feet and extending the digits, and drops

clear of the surrounding bats. After dropping a foot or less the bat pulls upward in a shallow arc and begins level flight. This method often is used by a bat that is hanging alone. Instead of beginning level flight after dropping clear of the bats hanging nearby, an individual sometimes hovers immediately beneath the group for a few seconds and then alights at a point only a few inches away from its former roosting place. The second method of launching is generally used when a bat makes a short flight during which it remains only a few inches below the ceiling. While the feet retain their grip on the ceiling and the head is elevated, the wings are spread and make several rapid strokes; this swings the body in the direction of the bat's dorsal surface and tends to bring the body nearly parallel to the ceiling. The bat then releases its hold on the rock and immediately begins nearly level flight. The bat drops only slightly away from the ceiling, and to an observer seems suddenly to begin level flight from a hanging position. Frequently when *Macrotus* takes flight in this way the wings can be heard rustling against the ceiling.

This bat often hovers, both when foraging and when flying in its daytime retreat. *Macrotus* seems to hover easily, and is able to hover for several seconds at a time. On many occasions, while I was watching groups of leaf-nosed bats at their daytime roost, individuals flew down to within a foot or two of my face and hovered there for several seconds as they did also at night. Hovering is accomplished by flying upward with just enough force to counteract the pull of gravity. The body is nearly vertical to the ground, the legs are pulled laterad and the uropatagium is spread as fully as possible, while the wings make rapid but shallow beats. The ears are erect and the head is pointed toward whatever occupies the bat's attention.

In early June, 1953, two miles south of Vidal, Riverside County, in a deserted cabin on the border of a dry wash supporting scattered examples of palo verde, catclaw, smoketree, ironwood and mesquite, *Macrotus,* together with pallid bats (*Antrozous pallidus*), big-eared bats (*Corynorhinus townsendii*), cave myotis and Yuma myotis (*Myotis yumanensis*) roosted at night. In the three-day period of my stay there, the locality was a favorite foraging area for numbers of leaf-nosed bats, and they could be observed easily by flashlight as they flew over the wash or the nearby desert. These bats regularly foraged here as elsewhere within three feet of the ground. They often dropped down nearer the surface of the ground and occasionally hovered there for a few seconds. They frequently

foraged close to vegetation and seemed not to slacken speed when approaching obstacles, but avoided them easily and gracefully. Even bats released in the daytime flew fairly close to the ground. One individual liberated in this area in the daytime flew roughly 300 yards before being lost to view and was never seen to fly higher than approximately ten feet above the ground.

Leaf-nosed bats seem to be totally insectivorous, and their food clearly reflects the bats' foraging habits. Some insects regularly eaten by *Macrotus* are almost certainly taken from the ground or from vegetation. The stomachs of these bats taken in the summers of 1953 and 1954, in the Riverside Mountains, contained fragments of orthopteran insects, noctuid moths and caterpillars, and beetles of the families Scarabaeidae and Carabidae, together with unidentified material. The wings of sphinx moths (Sphingidae), butterflies and dragonflies were found beneath several night-roosts of *Macrotus*. Beneath roosts in Imperial County, California, Huey (1925) found remains of grasshoppers, sphinx moths, noctuid moths and beetles. The flying insects mentioned above could possibly have been caught while they were on the wing, but more likely were taken while resting. This supposition is supported by Huey's (*op. cit.*) finding willow leaves (*Salix* sp.) beneath the roost of leaf-nosed bats and Stager's (1943) finding a dead leaf-nosed bat on a spiny desert shrub (*Eucnide urens*). H. W. Grinnell (1918:257) mentions that a leaf-nosed bat was captured in a mouse trap set on the open desert near Mecca, Imperial County, California. The lists of food items of *Macrotus* contain a preponderance of insects that seldom fly, are flightless, or that fly in the daytime; this constitutes strong evidence that this bat takes mostly insects that are on the ground or on vegetation. Assuming that *Macrotus* does so forage, its mode of foraging can be seen to be particularly effective in arid regions where there is little ground cover and where most of the vegetation has sparse foliage. Nocturnal insects moving along the open sandy or gravelly floor of the desert would be vulnerable to predation by a bat flying just above the surface of the ground, and insects clinging to sparse foliage would not be well protected.

Macrotus frequently alights to eat its prey and therefore probably does not forage continuously for long periods of time. Because some of the food items taken by this bat are fairly large, a small number of captures may suffice to fill its stomach. On several nights I watched a number of *Macrotus* returning to their daytime roost in order to eat insects they had just captured. On June 11, 1953, I observed this behavior at a large grotto used as a daytime roost

and nighttime roost by leaf-nosed bats. From 8:08 P. M., by which time all of the bats in the grotto had begun to forage, until 9:00 P. M. there was an intermittent traffic of bats flying in and out of the grotto. It was my impression that during this period bats were foraging near the grotto and returning to the roost to eat the larger insects, and then leaving to do more foraging. At the cabin two miles south of Vidal, San Bernardino County, these bats often alighted beneath the eaves of the cabin where they stayed for only a short time, probably to eat recently-caught prey.

Indirect evidence suggests that *Macrotus* has a small foraging range. They foraged over the floodplain of the Colorado River roughly one mile from the nearest place where *Macrotus* could roost, and at a cabin approximately one and one-half miles from the nearest known daytime roost. I saw none at the town of Vidal, about three miles from the nearest known roost. On a number of evenings, constant activity around a daytime roost suggested that *Macrotus* was foraging nearby, perhaps within a few hundred yards of the roost.

At all localities where records were kept of the times of emergence in the evening of the various local bats, *Macrotus* emerged last. The first individuals of this genus to begin foraging usually left their roosts no earlier than at dark, roughly one hour after sunset; this was usually about an hour and a half after the first western pipistrelles (*Pipistrellus hesperus*) appeared. The earliest recorded emergence for *Macrotus* was 7:40 P. M., 51 minutes after sunset, when a group of six left a grotto in the north-facing wall of a canyon. Because of the depth of the canyon and the steepness of the slopes the illumination was considerably lower here than at many other roosts at a comparable time in the evening. The members of small groups of *Macrotus* often left their daytime retreats together, or nearly so, but taking all of the records into account, it seems that the time of emergence of *Macrotus* in the evening is spread out over approximately three hours. On a number of nights I spread a silk "mist net" across the mouths of various caves and mine tunnels and kept record of each bat captured, its time of capture, and, when the animal was killed and saved for a specimen, the amount of food in its stomach. Because the net was taken down periodically to allow the passage of large groups of *Myotis velifer*, the stomach of each *Macrotus* was checked before it was counted as having just emerged. Some of the bats that hit the net from inside the caves probably were simply making short flights preparatory to leaving

the roost, but in general the records of times of emergence obtained by this method agreed with those gained by direct observation of colonies. Leaf-nosed bats generally began striking the nets slightly after one hour after sunset, and the frequency of captures was greatest from roughly one hour and fifteen minutes after sunset to two hours after sunset (approximately 8:05 P. M. to 8:50 P. M.). Many leaf-nosed bats with empty stomachs were taken as late as two hours and fifteen minutes after sunset, and one bat having only a trace of food in its stomach was caught three hours and four minutes after sunset (9:51 P. M.). The pre-midnight foraging period lasts until about four hours after sunset (11:00 P. M.). That is to say, most of the leaf-nosed bats forage sometime between one hour after sundown and four hours after sundown, and then retire to a night-roosting place. Actually, each bat seems to have a pre-midnight foraging period of roughly one hour. Only part of this time is spent foraging, because the bats alight to eat the larger insects.

In the middle of the night *Macrotus* hangs in some retreat and rests. It is less selective in choosing nighttime roosts than in selecting daytime roosts; adequate overhead protection seems essential, but a wide range of structures are occupied at night—old adobes, deserted wooden buildings, cellars, porches, and a wide variety of caves, mine tunnels and grottos.

In the early morning there is a second foraging period beginning shortly after midnight, probably around 1:00 A. M., and not so clearly defined as the pre-midnight period. Although some bats become active at about 1:00 A. M., some four and one-half hours before sunrise, many rest until around 3:00 A. M., one and one-half hours before sunrise. The greatest activity in early morning seems to occur between two and one-half hours before sunrise and thirty minutes before sunrise. Bats generally begin returning with full stomachs to their daytime roosts about two hours before sunrise, and the last bats usually return approximately twenty minutes before sunrise. A pronounced increase in *Macrotus* activity occurs roughly forty-five minutes before sunrise, and suggests that many bats wait until fairly late to fill their stomachs preparatory to returning to their daytime roosts. Light-tolerance of this bat possibly differs in the morning from that in the evening. Usually there is some activity of leaf-nosed bats through the early morning hours, but I doubt that the early-morning foraging period of each bat is longer than forty-five minutes. Many bats probably forage for considerably less time than this, for in the summer when large prey

items such as grasshoppers and large crickets are common, a part of the total time spent by *Macrotus* in filling its stomach must be occupied by eating the large food items while the bat hangs in some sheltered place. It is, of course, difficult to estimate the amount of time spent by this bat in traveling from its daytime roost to its nocturnal foraging area, and this would add to the length of the activity period. Considering all of these points, one hour and forty-five minutes is a reasonable estimate of the maximum amount of time spent on the wing by *Macrotus* on a summer night.

AERODYNAMIC CONSIDERATIONS

According to Savile (1957:212) "The form of a bird's wing is so basically important to the successful exploitation of an ecological niche that it inevitably yields many instructive examples of adaptive evolution." The same could be said of the chiropteran wing, and as a basis for the anatomical discussions to follow it is necessary to consider briefly the aerodynamic significance of certain forms and functions of the wings of the bats under consideration here.

Poole (1936) showed that most bats have lower wing loadings than do birds, and he mentioned that this difference may be due to the way in which many bats forage. (Poole used the number of square centimeters of wing surface per gram of body weight in his measurements of wing loadings; following standard engineering practices, I have measured the loadings in pounds per square foot, and have assumed that the wings were continuous through the

TABLE 1. AERODYNAMIC CHARACTERISTICS OF THE WINGS OF THE BATS STUDIED.*

Species	Weight (g)	Wing span (mm.)	Wing loading (pounds per square foot)	Aspect ratio (span²/area)	Ratio of proximal to distal segment of wing (area)	Uropatagial loading (pounds per square foot)
Eumops perotis.....	55.0 (5)	516 (4)	.51 (4)	11.9 (4)	68.8 (4)	4.5 (3)
Myotis velifer.....	8.6 (20)	249 (6)	.19 (6)	6.8 (6)	78.8 (6)	1.4 (3)
Macrotus californicus	14.1 (12)	295 (6)	.23 (6)	6.8 (6)	80.3 (6)	2.1 (3)

* The measurements from which the above data were obtained were taken from specimens in alcohol; thus, although the table shows in general the comparative aerodynamic characteristics of the wings it does not necessarily give the values that would be obtained from fresh specimens. The figures are all averages, and the numbers of specimens upon which the averages are based are given in parentheses.

bodies.) Most insectivorous birds forage by making repeated, short flights. Bats, on the other hand, remain on the wing for most if not all of the time they are foraging, and insects are captured by virtue of the bat's ability to maneuver rapidly. A light wing loading enables bats to fly with fair economy of energy for long periods of time at low speeds, and the large flight surfaces are of great help in turning abruptly and in maneuvering while capturing insects. The small sizes of most insectivorous bats favor low wing loadings because the ratio of mass to surface area is small (the volume and mass vary as the cube of the linear dimensions, whereas the surface area varies as the square). If bats had as great a size range as birds, the wing loadings of the two groups probably would more nearly resemble each other. In birds the slots formed by the alula and primary flight feathers allow these animals to have high wing loadings and fairly low stalling speeds. The unslotted wings of bats do not yield such refinements in flight characteristics, but within the range of size and wing loadings found in bats there is little need for increasing lift. In one respect the flight of bats is clearly less efficient than that of birds. The upstroke consumes relatively more power in bats than in birds because the wing-surfaces in bats are continuous and do not allow the passage of air as do the spaces between the primaries of a bird. It is probable, however, that differences between the wing loadings of birds and insectivorous bats reflect primarily the demands of the foraging habits of bats.

Wings of most bats are airfoils of high camber (anteroposterior curvature) and lateral camber (decrease of the dihedral from the base to the tip of the wing). In terms of lift, this type of wing is efficient at low speeds. The wing membranes are irregular in shape and the part of the wing composed of the propatagium (the membrane anterior to the humerus and radius) plus the plagiopatagium (the membrane posterior to the humerus and radius and between the fifth digit and the body and hind limb) has a greater surface than the chiropatagium (the membranes between the digits), which narrows distally and has its leading edge gently swept back. Camber of the wing is produced by flexion of the digits, particularly the fifth, the position of the hind limb, which anchors the posterior edge of the plagiopatagium, and by the angles that the propatagium and dactylopatagium minus (the membrane between the second and third digits) make with the posterior parts of the wing membranes. During flight the air pressure against the ventral surfaces of the wing membranes is greater than that against the dorsal surfaces; this helps to maintain a smooth camber. The wings seem makeshift

and inefficient due to their irregular shape, but this irregularity is the source of increased efficiency in certain parts of the wing. The tapering distal part of the wing gives the wing a fairly high aspect ratio (ratio of the length of a wing to its width; in wings of irregular outline the aspect ratio is considered as the ratio of the square of the wing span to the total wing area) and serves to reduce the turbulence and loss of lift at the end of the wing as it passes through the air (this loss of lift is called "end effect"). The proximal part of the trailing edge of the plagiopatagium merges fairly evenly into the calcar portion of the uropatagium, thereby producing a smooth transition from wing-base to tail membrane and tending to avoid turbulence and drag at this point of junction. Bearing in mind the basic pattern of the wing of the bat, it is instructive to compare the wings of the three bats under discussion using as a basis certain simple aerodynamic principles plus what is known of the flight of birds having similar wings.

The wing of *Eumops* is long and slender, and has many of the characteristics known in birds to be associated with rapid and enduring flight. Compared to the other two bats the wing of *Eumops* has low camber. In the proximal segment of the wing the low camber results in part from a relatively narrow propatagium that is inclined downward at only a moderate angle, and in the chiropatagium the low camber is caused by the small size of the dactylopatagium minus, which is inclined downward at only a slight angle to the rest of the chiropatagium. A fairly low camber is typical of high-speed wings in birds and serves to reduce drag. The chiropatagium is less broad than the proximal segment of the wing and tapers to a narrow rounded tip. The tip of the wing, starting from the end of the fourth digit, is shaped strikingly like the distal part of the notched primary wing feather of a bird. By reducing the end effect, the notched primaries of birds increase the lift produced by a wing. Likewise, the slender wing-tip of *Eumops* reduces the loss of lift at the wing-tip due to the end effect. The shape of the posterior edge of the plagiopatagium is such that it blends smoothly with the uropatagium and probably little turbulence is created at this point. The anterior edge of the propatagium curves forward near its base, creating a fairly smooth junction with the body. The remarkably high aspect ratio of the wing of *Eumops* is strong evidence indicating that this bat is adapted to fly for long periods of time at a moderately low energy output. The aspect ratio of the wing of the mastiff bat is considerably higher than that of the herring gull (*Larus argentatus*) and is thus probably above that of

most gulls. A long wing of high aspect ratio has been developed by various sea birds noted for their ability to soar (gulls, gannets, albatrosses). It is interesting to note that like *Eumops* some birds with high-aspect-ratio wings have difficulty taking off from flat surfaces, and need to take off into a wind or launch themselves from a cliff. Certain birds capable of rapid flight, such as the golden plover (*Pluvialis dominica*) and chimney swift (*Chaetura pelagica*) have high-aspect-ratio wings (Savile, 1957:215). While it is doubtful that *Eumops* does any soaring, it is known that this bat's flight is rapid, and the aerodynamic efficiency of its wings is probably correlated with the animal's ability to fly for prolonged periods.

Although their description does not logically belong in a study of appendicular morphology, the axial parts of the bats deserve mention here because of their aerodynamic importance. *Eumops* has large ears, and at first glance it seems that they would serve as funnels and would produce considerable drag during flight. Upon close examination, however, the ears can be seen to be crude airfoils that function as lifting surfaces during flight. Compared to most bats the head of *Eumops* is extremely large and the dentition is robust, and yet the neck, which would be expected to support the head during flight, is not particularly heavily built and seems hardly adequate to support the head throughout long flights. When this bat is in flight, in fact whenever the animal is not alert to danger or looking at nearby objects, the thick, flat keels at the ventral bases of the ears cover the eyes and lie along the sides of the head (Fig. 1), and the broad ears face ventrolaterad with the pinnae extending laterad. In this position, the ears resemble short, stubby wings, even to the dorsal arching (camber) of the pinnae and the continuous leading edge. Because of their shape and position with respect to the direction of flight, the ears produce lift during flight, and this tends to raise the head. The lift supplied by the ears probably has the important function of tending to hold up the head, thereby supplementing the action of the muscles that elevate the head. To a bat that has a large head and flies for long periods of time any such conservation of energy would be advantageous. The position of the ears in *Eumops* is characteristic of many of the members of the family Molossidae; in this position the ears produce a minimum of drag during flight, this being of importance in a group of bats that fly rapidly and many species of which fly for long periods of time.

The head, the dorsally arched body and the uropatagium of *Eumops* form a crude airfoil of high camber. In this bat the fairly

flat head, the long shallow body and short but moderately broad uropatagium seem to form a more conventional airfoil than that formed by the corresponding parts of the other genera. The heads and bodies of *Myotis* and *Macrotus* are fairly deep and the uropatagial membranes are larger than that of *Eumops*. The airfoil formed by the head, body and uropatagium of *Eumops* is a more nearly flattened section than the airfoils formed by the corresponding parts of the other genera, and is better adapted to rapid flight. It is known that the body of an airplane often supplies considerable lift; in some cases this amount of lift is greater than the amount that would be produced by an equally broad section of wing. Taking this into account, it is probable that in a bat the head-body-uropatagial section contributes a significant proportion of the lift produced by the animal in flight.

The uropatagium is important as a braking surface as well as a lifting surface, and, other things being equal, the larger the uropatagium in relation to the total weight of the bat the greater the ability to maneuver. In *Eumops* the loading of the uropatagium (ratio of weight of bat in pounds to surface area of uropatagium in square feet) is higher than in the other two genera. Compared to these bats the wing loading of *Eumops* is also higher, and this demands greater flying speeds and supplies less surface for braking in connection with sudden changes of direction. Thus it would be supposed that *Eumops* flies more rapidly and less maneuverably than the other two bats. Observations in the field support this supposition.

Relative to *Eumops*, the wings of *Myotis velifer* are not as long and slender, and they have the characteristics usually associated with a low-speed, high-lift wing. The camber of the entire wing is high because of the large propatagium that is pulled downward at a fairly sharp angle to the plagiopatagium, the relatively large dactylopatagium minus that extends downward at an angle to the rest of the chiropatagium, and the long fifth digit, the phalanges of which are flexed fairly strongly ventrad during flight. The tip of the wing is tapered abruptly and probably tends to avoid the end effect, but seemingly considerably more lift is lost at the wing-tip of *Myotis* than at the slender wing-tip of *Eumops*. Because of the pronounced taper of the distal half of the chiropatagium the wing has a fairly high aspect ratio. The high camber of the entire wing and the breadth of the proximal segment of the wing clearly indicate that the wing is adapted to low flying speeds. *Myotis velifer* has a lower wing loading and the uropatagium is much

larger relative to the body weight than in the other genera; thus it has large flight surfaces that allow high maneuverability. The wing loading of this bat is below that of any bird on which I can find data available in the literature. Even allowing for the inefficiency of the upstroke of the wing-beat cycle in bats, the characteristics of the wing of *M. velifer* indicate that it is probably better adapted than any bird to low-speed, highly maneuverable flight at a moderate level of energy output. The mode of foraging of this small bat would seem to demand such adaptation.

The wings of *Macrotus* are relatively shorter and broader and of higher camber than the wings of the other two bats, and are adapted to low-speed flight and high maneuverability. The propatagium and dactylopatagium minus are large, and during flight are pulled sharply downward at an angle to the more posterior parts of the wing membranes. The fifth digit is longer relative to the other digits than in the other genera, and the phalanges retain considerable ventral flexion during flight. The wing loading is far lower than in *Eumops* and but slightly higher than in *Myotis velifer*, and the aspect ratio is the same as that of *M. velifer*. Thus, in terms of general aerodynamic characteristics, *Macrotus californicus* closely resembles *Myotis velifer*. In the former the shape of the distal part of the wing is such that more lift is lost due to the end effect than in the other genera. The large ears, which face almost directly forward during flight, the short, deep body, and the posture of the hind limbs make these parts of the animal form a far less efficient airfoil than is formed by the corresponding parts in the other two bats. *Macrotus californicus* seems to spread its uropatagium widely (by spreading the legs apart) only when hovering or performing other maneuvers requiring a departure from straight level flight. The loading of the uropatagium is greater than in *Myotis velifer* but is less than half that of *Eumops perotis*. Judging from aerodynamic considerations of *Myotis velifer* and *Macrotus californicus*, the former might be expected to be more maneuverable than the latter. This is known not to be the case, and the extreme maneuverability of *M. californicus* is probably largely due to the specializations of its sensory equipment.

The proportions of the segments of the wings of the three bats show considerable variation. The area of the chiropatagium is larger relative to that of the proximal segment of the wing in *Macrotus* than in the other genera. This ratio may simply be a result of the greater degree of taper in the wings of *Eumops* and *Myotis*, and hence their greater efficiency in the utilization of lift. Relative to the proximal segment of the wing, the chiropatagial seg-

ment is much longer in *Eumops* than in the other bats. Perhaps this reflects a reduced dependency on flapping flight in *Eumops,* for in birds, as a general rule, elongation of the distal segments of the wings relative to the total length of the wing and of the body is associated with soaring flight, whereas relatively short distal segments are found in species using predominantly flapping flight (Fisher, 1955:84). This generality has many exceptions among the birds; applied to the bats here considered, however, it may find some support, since observations of these bats in the field indicate that *Eumops* does beat its wings more slowly than do the other bats, and, at least when landing and taking off, performs dives and rapid glides during which the wings are set and do not beat.

OSTEOLOGY

Introductory Remarks

Bats normally hold their forelimbs more or less out from the sides of the body and not vertical to the substrate as do cursorial mammals. Therefore, the dorsal surface of the humerus in bats corresponds to the lateral surface in most mammals. The carpus of bats is so modified that the manus is always in a partly supinated position; the palmar surface is directed mediad (or ventrad, when the wing is extended to the side). Hereinafter, descriptive terms are applied to the forelimbs of the bats under study as these terms are applied to the forelimbs of other mammals, by assuming that the forelimb is oriented vertically to the substrate. Regarding the manus, however, the descriptive terms are applied as if the limb were held outstretched laterally as it is when extended for flight. Thus, the pollical side of the manus is termed the anterior side and the opposite side, the posterior side; the palmar surface is termed the ventral surface and the opposite surface, the dorsal surface.

The hind limbs of cursorial mammals are carried vertical to the substrate with the plane of movement of the joints directed anteroposteriorly. This is not the posture of the hind limbs in bats; in fact, none of the three bats under study is even able to bring its hind limbs into this position. When *Eumops* and *Myotis* are in level flight the hind limb is held out to the side, with the femur extending laterad and slightly dorsad at an angle of roughly 90 degrees to the long axis of the body. The shank extends caudad and slightly ventrad, but is approximately parallel with the long axis of the body. In *Macrotus* the position of the hind limbs during level flight differs even more from that in most other mammals. The hind limbs are held behind the bat in a spider-leg-like posture, with the femur ex-

tending dorsad and caudad, and with the shank partially flexed and extending caudad and more or less downward. In *Eumops* and *Myotis*, the hind limb during flight is as if it has been rotated 90 degrees from the position of the limb in cursorial mammals. In *Macrotus* the rotation amounts to nearly 180 degrees. Thus, the lateral surface of the shank in most mammals is homologous with the medial surface of the shank in *Macrotus*. In *Eumops* and *Myotis*, and in other bats that crawl with any facility, the hind legs are used in reptilian fashion, being held out to the side of the body rather than beneath it; the femur extends laterad and more or less dorsad from the body, and the shank is flexed at right angles to the thigh and is held roughly vertical to the substrate. The descriptive terminology will be applied in the same way to the hind limbs of the bats considered here as it is to the hind limbs of other mammals. It should be stressed, however, that these terms apply only when the hind limbs of bats are put in the posture typical for terrestrial mammals, and that normally the limbs of bats are not in these positions.

The discussions of the functional significance of many of the osteological specilizations found in bats are reserved for the section on conclusions.

The osteology of *Eumops* is described in some detail, whereas the osteological descriptions of *Myotis* and of *Macrotus* are essentially comparisons between the elements in those genera and in *Eumops*. When a bone is said to be larger in one bat, the bone is larger relative to the size of the body than is the corresponding bone in the other bat, or bats, used in comparison.

Vertebral Column

The bodies of most bats are short and thick as a result of the anteroposterior compression of the individual vertebrae and the marked dorsal arching of the thoracolumbar section of the vertebral column. In the three genera studied the arching is most pronounced in *Macrotus* and least so in *Eumops*. Owing mostly to the difference in arching, *Macrotus* is relatively short, broad and deep, *Eumops* is long, narrow, and shallow, and *Myotis* is intermediate.

The numbers of postcervical vertebrae in the three genera are as follows: *Eumops*, thirteen thoracic, six lumbar, five sacral, ten caudal; *Myotis*, eleven thoracic, five lumbar, five sacral, ten caudal; *Macrotus*, twelve thoracic, six lumbar, five sacral, seven caudal. Only thoracic, lumbar and sacral vertebrae are discussed; on them many appendicular muscles have their origins.

Thoracic Vertebrae

Eumops.—These vertebrae are roughly one half as long as high. The first is the largest of the thoracic series and each succeeding vertebra is smaller to the seventh thoracic, from which point caudad all the thoracics are approximately the same size. The centra of the first twelve thoracics are flat anteriorly

and posteriorly; those of the last two are procoelous. The centra are dorsoventrally compressed, and the dorsal surfaces are slightly concave. The vertebral foramen is largest in the first several thoracics, becoming progressively smaller toward the posterior end of the thorax. The laminar parts of the neural arches are nearly flat through the anterior half of the series, but become more strongly arched toward the posterior end of the column.

The neural spine on the first thoracic vertebra is prominent, broad, and knoblike, and provides part of the origin for the large anteriormost part of the trapezius group of muscles. On the second thoracic vertebra, a low medial neural ridge merges with two weak lateral ridges. They give rise to a pair of low tuberosities at the posterior edge of the laminar part of the neural arch. From thoracics two to six the medial ridge diminishes in size but the lateral ridges persist, joining medially to form a low neural ridge on the seventh thoracic. This ridge increases in breadth and height throughout the rest of the thoracic series.

In dorsal view, the anterior edges of the neural arches are concave, the posterior edges are convex, and there are spaces between the laminar parts of adjacent neural arches. These spaces are largest at the level of the fifth thoracic and become smaller both anteriorly and posteriorly from this point.

The short transverse processes extend dorsad and slightly laterad from the lateral edge of the nearly flat laminar part of the neural arches, rise above the highest parts of the arches in thoracics one to five, and become smaller toward the posterior end of the series. There are no transverse processes on the last four thoracics.

The zygapophyses of the first three thoracics are short and broad and the articular surfaces of the anterior zygapophyses face dorsolaterad. (The posterior articular surfaces always face in the direction reciprocal to that of the anterior articular surfaces.) The zygapophyses of thoracics four to eight are long and fingerlike. A small pointed tuberosity (metapophysis) extends craniad from the anterior surface of the top of the transverse processes of thoracics one to eight. The anterior zygapophyses project progressively more sharply dorsad toward the caudal end of the thoracic series, until, on the tenth thoracic, they unite with the metapophyses to form a large anterior articular process. The cranial articular processes of the last four thoracics, then, are formed partly by the anterior zygapophyses and partly by the metapophyses. The anterior articular surfaces are concave and the posterior surfaces convex, thus forming a strong but incomplete tongue-in-groove joint that probably limits dorsoventral bending of the vertebral column. The cranial articular surfaces face dorsolaterad in thoracics one to seven, roughly dorsad in thoracics eight and nine, and directly mediad in the rest of the thoracics. The last three thoracics bear accessory processes.

The articular facets for the tubercula of the ribs face laterad. The caudal demifacets are large, face caudolaterad, and are surrounded by bone much thicker than that comprising the rest of the pedicle. The cranial demifacets are smaller and less well defined than the anterior demifacets, but are similarly braced by thick bone. The ribs make contact not only with the main articular facets but also with the anterior parts of the pedicle to which the medial surfaces of the ribs between the tubercula and capitula are bound by fascia.

The caudal intervertebral notches are large at the anterior end of the thorax and extend craniad farther than the level of the middle of the centrum, but

become progressively smaller toward the posterior end of the thorax. The cranial intervertebral notches are small and are covered by the ribs.

The first thoracic vertebra is the largest of the thoracic series and merits special consideration. Its centrum and anterior zygapophyses are fused with the centrum and posterior zygapophyses of the last cervical vertebra leaving no trace of the former points of articulation. A few gaps remain between the laminar parts of the vertebrae; the intervertebral foramen is unconstricted. The large, dorsoventrally elongate facet for the articulation of the head of the first rib extends ventrad to the level of the slightly concave ventral surfaces of the fused vertebrae. The facet for the articulation with the tuberculum of the first rib is on the ventrolateral surface of the short, thick transverse process. The proximal part of the greatly enlarged first rib is in contact with most of the lateral surface of the first thoracic vertebra. The transverse processes of the first thoracic vertebra extend more nearly laterad than those of the rest of the thoracics and provide origin for the tendons of the anteriormost part of the trapezius group of muscles.

Myotis.—The spaces between the neural arches are relatively smaller; the transverse processes project more nearly laterad and persist throughout the thoracic series; the first thoracic and last cervical are not fused; fingerlike projections (metapophyses) extend anteriorly from the dorsal edge of the cranial articular processes of the last four thoracics and partly enclose the tops of the concave anterior articular surfaces. Although there is no bony fusion of the first thoracic and last cervical vertebrae, there is little movement possible between them. The intervening intervertebral disc is thin and the anterior articular surface of the first thoracic faces anteromediad and makes a tight junction with the posterior articular surface of the last cervical. Two bony projections from the posterior margin of the lamina of the last cervical make contact with the anterior margin of the lamina of the first thoracic and provide additional reinforcement.

Macrotus.—The thoracic vertebrae of this bat differ considerably from those of the other two genera. The spaces between adjacent neural arches are narrow and these, except for the last four, are bridged by two bony projections from the posterior edges of the lamina. The first thoracic is not fused with the last cervical and they fit together approximately as they do in *Myotis*. A pair of ridges, one on each side of the midline, occur on thoracics one to nine. These lateral ridges become smaller posteriad and converge to form a low medial ridge on thoracics eleven and twelve. The articular surfaces of the anterior zygapophyses face dorsomediad throughout the thorax and there is no tendency toward the development of a tongue-in-groove articulation anterior to the last thoracic. From the dorsal part of the anterior zygapophyses of this vertebra, fingerlike metapophyses extend over the dorsolateral part of the posterior zygapophyses of the eleventh thoracic.

Lumbar vertebrae

Eumops.—There are six lumbar vertebrae in this genus. In general they resemble the last four thoracics but are more robust and relatively longer. The lumbar centra are all procoelous. The intervertebral discs posterior to the last three lumbars are appreciably thicker than those of the thoracic vertebrae, and the intervertebral foramina become progressively larger toward the caudal end of the lumbar series.

The lateral surfaces of the centra of lumbars three to five bear low ridges that terminate caudally on each vertebra as small tuberosities. These ridges are inclined ventrad and caudad and considered together, form a ridge from the level of the top of the centrum on the anterior edge of the third lumbar to the ventral surface of the posterior edge of the centrum of the fifth lumbar. Dorsal to this ridge the lateral surfaces of lumbars three to five are flattened and give origin to the M. psoas major and M. iliacus. From the ridge itself the Mm. psoas major and minor take origin.

When viewed dorsally the tops of the neural arches are notched anteriorly and posteriorly, and only narrow spaces are present between adjacent arches. Broad, low neural ridges occur on all the lumbars; on the last two the ridges become spinelike and are inclined caudad.

The anterior zygapophyses of the lumbars are much like those of the last four thoracics but are larger, extend dorsolaterad, and their articular surfaces face dorsomediad. The posterior zygapophyses are broader and more robust than those of the last four thoracics.

Myotis.—This genus has five lumbar vertebrae. The lumbars are procoelous, but the curvature of the anterior and posterior surfaces of the centra is slight. No definite ridges are present on the lateral surfaces of the last few lumbars along the line of origin of the iliacus group of muscles. The ventral surface of the centrum of the fourth lumbar has a pair of low, rounded ridges, and the pedicle has a small tubercle that probably represents a transverse process. The last lumbar has a short transverse process that projects craniad and bears an extremely reduced neural ridge. Only the first lumbar bears accessory processes. The thickest intervertebral disc of the thoracolumbar series separates the centra of the last lumbar and first sacral vertebrae; the articulation is between two convex surfaces.

Macrotus.—This genus has six lumbar vertebrae and, as in *Myotis*, the centra are only weakly procoelous. In comparison to the other two genera, there are several characters of the lumbar vertebrae peculiar to this genus. A pair of ventral ridges occurs on the centra of lumbars four and five and the sixth lumbar bears a short, broad mid-ventral spine that projects craniad. Lumbars three to five have small transverse processes. The metapophyses are pointed and unusually large. The top of the neutral arch of the sixth lumbar is flat and shows no indication of a neural spine, but a cranially projecting transverse process is present. The sixth lumbar is strongly compressed anteroposteriorly; the posterior surface of its centrum and the anterior surface of the first sacral centrum are both convex and produce a joint that allows considerable movement.

Sacral Vertebrae

Eumops.—The four sacral vertebrae are completely fused. They remain roughly the same breadth as the posterior lumbars, but, starting with the first sacral, are abruptly compressed dorsoventrally in the parts beneath the transverse processes; as a result the last sacral is approximately three fifths as high as the lumbars. The diameter of the vertebral canal is greatly reduced toward the caudal end of the sacrum. The sacral foramina are distinct, becoming smaller caudally. The neural spine of the first sacral is low and thick and resembles, in general, the spine of the last lumbar; the spines of the

rest of the sacrals are thin but are higher and longer than those of the lumbars. Only the bases of the neural spines are fused. The zygapophyses of the first sacral are roughly the same as those of the lumbars but bear no metapophyses. The transverse processes are fused to form a broad lateral mass that is thick in sacrals one and two and thin in the last two sacrals. The thick part of the lateral mass is fused to the ilium; the fusion is continuous and extends from the crest of the ilium to a point approximately 2 mm. anterior to the level of the acetabulum.

Myotis.—There are four sacral vertebrae. Neural spines on the first two are more nearly fused and the lateral masses of these vertebrae are relatively thinner than in *Eumops.*

Macrotus.—The sacrum of this genus differs from that of the other two genera as follows: composed of five vertebrae the last of which is incompletely fused with the fourth; in dorsal view the last three sacrals are much narrower than the first two; intervertebral foramina are more strongly reduced; neural spines of the first four sacrals fused, forming a low, thin crest from which the neural spine of the last sacral is separate; sacrum is more lightly built and is arched slightly ventrad.

Sternum

Eumops.—The sternum is composed of three bones separated by discs of cartilage. The longest element is the body of the sternum, the manubrium is slightly shorter, and the xiphoid process is the shortest part.

Viewed ventrally the manubrium looks like an asymmetrical cross. The manubrium has two short lateral arms, a slightly longer anterior arm, and a still longer posterior arm. The anterior arm is clavate as viewed from the side and is laterally compressed. It is inclined ventrad and forms an angle of approximately 30 degrees with the long axis of the posterior arm. The lateral arms are short and thick, roughly triangular in cross section, with one flat surface facing ventrad. The lateral arms curve gently dorsad; their distal ends are expanded and terminate in flat articular surfaces that face anterolaterad and against which lie the sternal ends of the clavicula and first costal cartilages. The posterior arm of the manubrium is roughly circular in cross section; its dorsal surface is flattened and the posterior end is expanded and truncate. A low, inconspicuous ridge extends the length of the ventral surface of the manubrium.

The body of the sternum is straight and nearly circular in cross section anteriorly, becoming increasingly dorsoventrally flattened caudally. The anterior end is expanded and smooth, and meets the smooth posterior articular surface of the manubrium. A heavy band of connective tissue binds together the ventral part of this joint, whereas the dorsal part of the joint is free to gape open slightly. This creates a hinge joint that allows the posterior part of the sternum to swing ventrad but does not allow it to move dorsad beyond the point at which it is in line with the posterior arm of the manubrium. There are small tubercles on the lateral surfaces of the body of the sternum to which the costal cartilages of ribs three to seven attach. A low, poorly defined ridge extends the length of the ventral surface of the body. The anterior half of the xiphoid process is narrower than the posterior end of the body of the sternum and is approximately square in cross section. The xiphoid

process becomes progressively broader and more dorsoventrally flattened caudally; the posterior third is cartilaginous. The cartilaginous extension is broad and flat and the posterior margin is rounded. The connection between the body of the sternum and the xiphoid process allows but little movement.

Myotis.—Two separate elements make up the sternum of this genus, an anterior part, the manubrium, and a posterior part consisting of the fused body of the sternum and the xiphoid process.

The manubrium is approximately half as long as the posterior part of the sternum. As seen ventrally the manubrium is T-shaped. The anterior arm is roughly as long as the posterior part and is laterally compressed; it projects ventrad at nearly right angles to the posterior arm and therefore is seen endwise when the manubrium is viewed ventrally. The lateral arms are broad, dorsoventrally flattened, and project slightly dorsad. The distal ends are thickened and bear flat articular surfaces that face craniolaterad. The posterior arm is broad and dorsoventrally compressed. A thin ridge extends from the posterior surface of the anterior arm of the manubrium to the posterior end of the ventral surface of the posterior arm.

In general shape the posterior part of the sternum in *Myotis* and *Eumops* is nearly alike. In *Myotis* costal cartilages three to six attach to the lateral surfaces of the body of the sternum. A low ridge extends along the entire ventral surface of the body of the sternum and along most of the ventral surface of the xiphoid process. The posterior end of the xiphoid process has a short, cartilaginous extension.

Macrotus.—The sternum in this genus consists of a manubrium and a single posterior part which represents the fused body of the sternum and the xiphoid process.

Discounting the cartilaginous caudal extension on the xiphoid, the manubrium is less than half as long as the posterior part of the sternum. Viewed ventrally the manubrium is approximately twice as broad as high and is shaped like a "T," with the lateral arms flared upward and the vertical bar shortened. The part of the manubrium that extends craniad in *Eumops,* and that here is termed the anterior arm, extends ventrad in *Macrotus* at approximately right angles to the long axis of the posterior arm and is therefore seen endwise when the manubrium is viewed ventrally. The anterior arm is short and broad anteroposteriorly, but is laterally compressed. From the middle of the ventral edge of the anterior arm, a thin keel extends directly posteriad to the caudal end of the posterior arm of the manubrium. The lateral arms arch gently dorsad and craniad; they become broader distad and are dorsoventrally compressed. The articular surfaces for the bases of the clavicula face anterolaterad from the expanded ends of the lateral arms. The posterior arm of the manubrium is short, not so broad as the other arms, and is dorsoventrally compressed. It has a prominent keel on the ventral surface. The posterior end of the posterior arm is truncate and by means of a movable joint articulates with the anterior end of the body of the sternum.

The body of the sternum is narrow and straight, flattened on its dorsal surface, and bears a high ventral keel that extends along the entire posterior part of the sternum. The keel is highest at the middle of the posterior part of the sternum and gradually diminishes in height craniad and caudad from this point. Costal cartilages three to seven connect onto the lateral surfaces

of the body of the sternum. The xiphoid process becomes only slightly broadened at its posterior end and gives way to a large, bifurcate cartilaginous extension.

Ribs

In the bats under study the rib cages are large compared, for example, to those of rodents of comparable sizes, and are broader than deep. The rib cage of *Eumops* is long and shallow, whereas that of *Macrotus* is relatively short and deep. In terms of shape, the rib cage of *Myotis* is roughly midway between these extremes. *Eumops* has thirteen ribs; the first seven are vertebrosternal, the next four are vertebrocostal, and the last two are vertebral. The corresponding arrangement in *Myotis* is eleven, six, three, and two; in *Macrotus* it is twelve, seven, three, and two.

The ribcages of all three genera have certain characteristics in common. The first rib is short but is considerably thicker and more strongly built than the other ribs. It is anteroposteriorly compressed and the entire medial surface of the elongate proximal end of the rib, from the tuberculum to the capitulum, is in contact with the lateral surface of the anterior part of the first thoracic vertebra. The first costal cartilage is the broadest and thickest of the series and attaches to the lateral arm of the manubrium. The first three ribs are more or less anteroposteriorly compressed, whereas the rest of the ribs are flattened in the opposite plane. When viewed laterally, the shafts of the ribs seem to be broadened by thin margins of bone that extend craniad and caudad from the thicker central part of the shaft. In *Eumops* the inner surfaces of ribs four through eleven are reinforced by a thin ridge of bone; in cross section, the anterior ribs are roughly T-shaped but the posterior ribs become triangular. In all three genera the ribs are two headed excepting the last two or three, in which the heads tend to merge. The tubercula articulate with the transverse processes and the capitula contact the articular facets of the centra; in addition, the entire medial surfaces of the proximal ends of the ribs, from the tuberculum to the capitulum, are in contact with the vertebrae.

Pectoral Girdle and Limb

Scapula

The scapulae in these bats lie dorsal to the ribcage with their long axes roughly parallel to the vertebral column.

Eumops.—The scapula is long (breadth approximately 40 per cent of length) and the post-spinous part is irregularly trapezoidal as viewed dorsally. The round anteromedial border of the supraspinous fossa gives way laterally to a deep suprascapular notch. The scapula is broadest anteriorly, at the level of the glenoid fossa, and becomes narrowed caudally. The supraspinous fossa is roughly one third as large as the infraspinous fossa. The entire rim of the scapula is thick, but the intervening surfaces are mostly thin and semitransparent. The axillary border and the part of the scapula between the glenoid fossa and the bases of the acromion and coracoid processes are especially heavily reinforced by thick bone.

The glenoid fossa faces almost directly laterad. It is irregularly shaped and is elongate anteroposteriorly. The broad part is posterior and the narrow part anterior; the dorsal edge of the fossa is concave and the ventral edge is straight. A large, blunt-pointed supraglenoid tuberosity projects laterad from

the anterior rim of the fossa. There is a smooth depression in the dorsal surface of the scapula just medial to the anterior part of the glenoid fossa against which the greater tuberosity of the humerus rests when this bone is flexed and raised. A low infraglenoid tubercle arises from the thick axillary border of the scapula 2 mm. posterior to the glenoid fossa.

The supraspinous fossa is inclined ventrad so that its flat dorsal surface faces anteromediad and is at an angle of roughly 145 degrees to the plane of the post-spinous part of the scapula. A narrow rim extends ventrad from the lateral border of the fossa. This rim enlarges anteriorly into a flat flange that extends ventrad at approximately right angles to the plane of the post-spinous part of the scapula. The flange increases in breadth and thickness anteriorly and is roughly triangular as seen from the front.

The low scapular spine is not perpendicular to the plane of the post-spinous part of the scapula but inclined slightly craniad. The lateral edge of the spine is thick and bears a long acromion process. A ligamentous sheet spans the gap from the medial edge of the spine to the dorsal part of the medial end of the acromion process and provides additional surface for the attachment of the Mm. supraspinatus and infraspinatus. The acromion is thick proximally and narrows distally; from the middle of its lateral surface projects a short metacromion process. The rounded distal tip of the acromion is flattened on its ventral surface where it contacts the distal end of the clavicle.

The long coracoid process arises from the anterolateral angle of the scapula. The coracoid projects ventrad for roughly one third of its length, then it turns and the distal two thirds extends ventromediad and slightly caudad. The tip of the coracoid is ventral to the lateral part of the suprascapular notch. The flat proximal third of the coracoid is broad as seen from the front; the distal two thirds is thinner, roughly elliptical in cross section, and the tip is expanded. From the lateral apex of the triangular flange of the supraspinous fossa a ligamentous sheet extends to the medial surface of the distal half of the acromion and the medial base of the coracoid. This sheet increases the area of origin of the M. supraspinatus.

The surface of the infraspinous fossa is divided into three facets that are set at angles to each other; the bone at the intersection of these facets is slightly thickened. This faceting serves to increase the area of origin of the Mm. infraspinatus and subscapularis. Working from the vertebral border laterad, the anteromedial facet faces caudolaterad and is tilted downward; the intermediate facet faces craniomediad and is tilted upward; the posterolateral facet faces caudolaterad and is tilted downward. As seen from above the intermediate and posterolateral facets are slightly concave and the anteromedial facet is convex. Viewed dorsally, the medial part of the infraspinous fossa is a broad trough formed by the anteromedial and intermediate facets; seen ventrally, the lateral part of the infraspinous fossa is a trough formed by the intermediate and posterolateral facets and a second trough is formed by the anteromedial facet of the infraspinous fossa and the entire supraspinous fossa. Extending caudad from the posterior end of the scapula is a cartilaginous extension that tapers to a point caudally. This extension provides extra surface for muscle attachment.

Myotis.—The scapula of this genus is slightly shorter and broader (breadth approximately 43 percent of length) and less strongly built. The supraspinous

fossa is roughly one quarter as large as the infraspinous fossa. The glenoid fossa faces laterad and slightly craniad; the supraglenoid tuberosity is less prominent. The surface of the supraspinous fossa is concave as viewed dorsally, is inclined only slightly downward, and the lateral rim is small. The scapular spine it low. The acromion is slightly shorter and bears no metacromion. The coracoid process is approximately the same breadth throughout its length; the proximal three quarters curves gently laterad and the distal quarter bends sharply laterad. The tip of the coracoid is ventral to the glenoid fossa. The posterior cartilaginous extension of the scapula is small.

Macrotus.—The scapula is less specialized than those of *Eumops* and *Myotis* and differs from them in many details. The scapula is shorter and broader (breadth approximately 50 per cent of length) and irregularly ovoid. The supraspinous fossa is considerably more than one third as large as the infraspinous fossa and is bounded medially by a small suprascapular notch. The glenoid fossa faces craniolaterad and the supraglenoid tuberosity is small. The supraspinous fossa has only a weakly developed rim and no anterior flange. The distal third of the acromion is flat and its finger-shaped tip extends ventrad to within roughly 0.5 mm. of the dorsal surface of the base of the coracoid. The broad, flat coracoid process curves steadily laterad and its tip extends beyond (lateral to) the glenoid fossa. There is no posterior cartilaginous extension on the scapula.

Clavicle

This element articulates proximally with the lateral arm of the manubrium in all three genera. In *Eumops* and *Myotis* the distal end of the clavicle is bound by ligaments to the dorsal base of the coracoid process and the ventral surface of the tip of the acromion process of the scapula; in *Macrotus* the clavicle is attached distally to the dorsomedial surface of the base of the coracoid process.

In *Eumops* the proximal third of the clavicle is nearly straight and is directed slightly forward, whereas the distal two thirds curves caudad. As seen from the front it is slightly S-shaped, with the proximal half curving ventrad and the distal half curving dorsad. The sternal base is large, nearly circular in cross section, with a smooth articular surface. As seen from above the clavicle is broad at its base, has a slight constriction just distal to the base, and becomes broader distally throughout the proximal third. The distal two thirds of the shaft becomes progressively narrower. The shaft is dorsoventrally compressed; the dorsal surface is slightly convex and most of the ventral surface is concave. The distal end is knoblike and inclined posteriad; its posterior surface is flattened.

The clavicle is more slender in *Myotis.* As viewed from above the shaft is is bow-shaped; it is curved throughout its length, the curvature increasing distally. The bone is S-shaped as seen from the front, but the curvature is less pronounced than in *Eumops.* The shaft remains nearly constant in breadth from end to end and is roughly elliptical in cross section, having the ventral surface slightly flattened.

The clavicle in *Macrotus* is similar to that in *Myotis,* but is more robust and is dorsoventrally compressed.

Humerus

In the bats considered here the humerus is long and slender and the ridges for muscle attachment are on the proximal fourth of the bone. The humerus is shorter and thicker in *Eumops* than in the other two bats. The diameter of the shaft is approximately 36 per cent of the width of the proximal epiphysis and 53 per cent of the width of the distal epiphysis; the diameter of the humerus is approximately 3.2 per cent of its length. Corresponding percentages for the other two genera are as follows: *Myotis*, 34, 37, 4.3; *Macrotus*, 33, 30, 4.3.

Eumops.—The head of the humerus is large and extends caudad from the posterior edge of the shaft a distance roughly equal to the diameter of the shaft. There is no neck; the head merges into the posterior part of the shaft and the tuberosities. If the humerus is viewed from the proximal end the head is ovoid and inclined mediad; the thickest part lies immediately posterior to the dorsal surface of the shaft, and the head extends craniad and mediad from this point to merge into the lesser tuberosity.

Immediately anterior to the head is a deep pit that is bounded anteriorly by the converging anterior ridges of the greater and lesser tuberosities and the proximal part of the pectoral ridge. The supraglenoid tuberosity fits into this depression when the humerus is extended to approximately a right angle with the lateral edge of the scapula. This arrangement serves as a locking mechanism to limit the forward movement of the humerus and prevent it from being extended beyond roughly a right angle with the body.

The greater tuberosity projects dorsolaterad well beyond the head of the humerus, is slightly flattened on its medial surface, and is broad and rounded as viewed laterally. Its anterior edge forms a ridge that continues distad to join the proximal end of the pectoral ridge. The entire medial surface of the greater tuberosity is smooth and forms an articular surface that merges posteriorly with the head and distally continues into the depression for the supraglenoid tuberosity. When the wing is flexed and raised, as it is in the upstroke of the wing-beat cycle, the medial surface of the greater tuberosity makes contact with a smooth-surfaced depression just medial to the anterior half of the glenoid fossa. This contact is made when the humerus reaches an angle of approximately 25 degrees above the plane of the scapula and locks the humerus at this angle. This tends to stop the upstroke by transferring its force to the scapula and the muscles binding the scapula to the body (see discussion of action of posterior division of M. serratus anterior). Miller (1907:13) thought that in some bats the greater tuberosity formed a secondary articulation with the scapula, thereby creating a strong joint at which movement was limited to a single plane. If movement were thus limited, the plane of movement of the humerus would be anteroposterior; this movement could not produce the wing beat. I am unable to understand Miller's reasoning on this point.

The lesser tuberosity does not extend beyond the head of the humerus, is thick proximally, becomes narrower toward its tip, and is connected by a thick ridge to the proximal end of the pectoral ridge. Distally the lesser tuberosity gives way to a prominent medial ridge that is turned slightly posteriad along its edge so that its posterior surface is concave. The lateral head of the triceps muscle takes origin partly from this concavity.

The pectoral ridge is strongly developed and projects craniad from the anterolateral surface of the humerus. The ridge starts at the distal base of the greater tuberosity and ends at a point slightly less than one quarter of the way along the humerus. The width of the ridge approximately equals the diameter of the proximal part of the shaft of the humerus. Viewed laterally the ridge is rounded anteriorly and reaches its greatest width roughly half way from its proximal to its distal end. The lateral surface is flat distally but slightly concave proximally; the anterior edge is broad and flat and extends mediad as an acute ridge posterior to which the medial surface of the ridge is concave and forms the lateral part of the bicipital groove. There is no lateral ridge on the humerus.

The shaft of the humerus is nearly straight, but its distal half curves gently craniad and dorsad. The lateral and medial surfaces of the distal half of the shaft become increasingly flattened distally. The distal quarter of the anterior surface of the shaft is flat. In the distal quarter of the posterior surface of the shaft a broad, shallow longitudinal depression is bounded laterally by a small ridge. The tendons and the distal sesamoid of the triceps muscles lie in this depression.

The distal epiphysis is displaced slightly anterior to the shaft of the humerus. The articular surface formed by the trochlea and capitulum is in line with the main axis of the shaft when viewed anteriorly. The capitulum is composed of two rounded ridges that are inclined laterad, slightly out of line with the main axis of the humerus, and separated by a groove. A second groove separates the medial ridge of the capitulum from the trochlea. This system of ridges and grooves extends from the shallow radial fossa around the anterior part of the distal articular surface. On the posterior side the grooves and ridges give way to a single broad groove with a low medial ridge; along this groove rides the pointed proximal end of the radius and the ventral part of the proximal end of the ulna. The lateral rim of the capitulum is prominent and is interrupted at the anterior edge of its proximal surface by a small tubercle. Immediately proximal to the tubercle is a shallow depression bounded posteriorly by a small ridge that extends along 1.5 mm. of the distal part of the shaft. From this ridge the Mm. extensor carpi radialis longus and brevis take origin. The medial epicondyle bears a curved spinous process, which extends distad beyond the trochlea. From the tip of this process originates the M. flexor carpi ulnaris. There is a fossa at either end of the pulley-shaped distal articular surface. The lateral fossa, which is surrounded by the rim of the capitulum, gives origin to the tendon of the M. supinator. The medial fossa is deep, extending nearly half way through the distal epiphysis, and serves as the surface of attachment for a thick ligament that extends from the fossa to the medial knob on the anterior end of the radius.

Myotis.—A careful description of the humerus of *Myotis* is given by Lawrence (1943). The humerus of *Myotis* differs from that of *Eumops* mainly in the following ways. The shaft is relatively thinner and the distal part curves more strongly craniad. The head is more nearly round, less ovoid, and projects caudad to the posterior surface of the humerus a distance greater than the diameter of the shaft. The pit for the supraglenoid tuberosity is shallower. Because of the placement of the glenoid fossa and the small size of the supra-

glenoid tuberosity, the humerus must be extended beyond an angle of 90 degrees with the lateral edge of the scapula before it is locked. The greater tuberosity does not extend so far beyond the head, and does not lock until an angle of roughly 30 degrees above the plane of the scapula is reached. The pectoral ridge is long and low; the anterior edge is straight and reaches its greatest height just short of its distal end. A low lateral ridge extends from the distal part of the greater tuberosity to just beyond the level of the distal end of the pectoral ridge. A small tubercle rises from the middle of the lateral ridge. The distal part of the shaft is not flattened on any surface. The distal articular surface is displaced farther out of line with the shaft of the humerus. The grooves on the distal articular surface of the humerus are shallower, as is the radial fossa. The notch formed by the depression immediately proximal to the tubercle on the rim of the capitulum is deeper. The spinous process of the medial epicondyle is shorter, extending only slightly beyond the distal articular surface. The fossae at the lateral and medial ends of the distal epiphysis are shallower.

Macrotus.—The humerus of this bat differs in many particulars from the humeri of the other two bats and seems less specialized than either. As seen laterally the distal part of the shaft curves gently forward; as viewed posteriorly it has a barely noticeable S curve, with the proximal end of the shaft curving mediad and the distal end laterad. The head is more nearly round; its longest axis extends from anterior to posterior. The head extends farther caudad from the posterior surface of the humerus. The pit for the supraglenoid tuberosity is shallower and does not limit the movement of the humerus until this element is extended well beyond an angle of 90 degrees to the lateral border of the scapula. The greater tuberosity extends only slightly beyond the head, and the humerus does not lock until it is raised to an angle of roughly 35 degrees with the plane of the scapula. The lesser tuberosity has a thicker, more nearly knoblike end. Near its distal end the ventral ridge bears a small thin tubercle. The shape of the pectoral ridge is similar to that in *Myotis,* but the ridge is lower; the anterior edge is thinner and does not help enclose the bicipital groove. The low lateral ridge angles across the humerus from the posterior edge of the dorsal surface of the greater tuberosity to a point immediately anterior to the middle of the dorsal surface of the humerus opposite the middle of the pectoral ridge. The distal part of the shaft is not flattened. As viewed anteriorly the distal articular surface is displaced so far laterad that the medial rim of the trochlea is nearly in line with the main axis of the shaft. There is no radial fossa. The ridges and grooves on the distal articular surfaces are only weakly developed. There is no depression at the medial end of the distal epiphysis. The medial epicondyle is large, irregularly anterioposteriorly flattened, and bears a short spinous process that does not extend to the distal edge of the distal articular surface.

Radius

Eumops.—The radius is long and thin and the proximal epiphysis is nearly twice as thick as the shaft. As viewed anteriorly the proximal epiphysis is triangular, and its most acute angle is directed proximad from the caudolateral surface of the radius. The triangular articular surface is inclined strongly

craniad and is deeply concave. It is marked by a central longitudinal groove that is bordered by two low ridges and a lateral and medial depression. Into the central groove fits the medial ridge of the capitulum of the humerus. There is a shallow smooth-surfaced depression in the posterior surface of the pointed proximal end of the radius; the proximal end of the ulna fits into this depression. Immediately distal to the anteromedial part of the distal rim of the articular surface is a deep slit that extends proximad and into which the tendons of the Mm. triceps brachii and brachialis insert.

The shaft arches forward gently, the curvature being greatest in the proximal half of the bone. Viewed anteriorly, the shaft curves slightly ventrad; this helps give horizontal camber to the wing. The shaft is largely circular in cross section and becomes slightly narrower distally; the distal half is flattened on its dorsal and ventral surface. The anterior surface of the distal three fifths of the radius is marked by a broad longitudinal depression in which lie the large tendons of the Mm. extensor carpi radialis and brevis. A second and narrower groove angles across the distal half of the radius from the posterolateral to the anterior surface. Along this groove passes the tendon of the M. abductor pollicus longus.

The distal epiphysis is slightly narrower than the proximal epiphysis. The articular surface of the distal epiphysis is deeply concave and is bordered anteriorly by two pointed processes; the lateral one probably represents the styloid process and the medial one an accessory process (pseudostyloid process). At the posteromedial rim of the articular surface is a broad, prominent process, and from the posterolateral rim a high, thin ridge extends proximad roughly 3 mm. from the articular surface. There is an elongate hole in the middle of the ridge and the distal end of the ridge forms a posterolateral continuation of the articular surface. This ridge provides a barrier between the tendons of the flexor and extensor muscles. On the anterior surface of the distal epiphysis, between and immediately proximal to the styloid and pseudostyloid processes, is a short broad ridge with concave sides and a weakly concave anterior surface. In the deep groove between this ridge and the pseudostyloid process lies the tendon of the M. abductor pollicus longus; over the anterior surface of the ridge passes the tendon of the M. extensor carpi radialis longus; through the groove between the ridge and a small tubercle on the anterodorsal surface of the epiphysis extends the tendon of the M. extensor carpi radialis brevis.

Myotis.—The proximal articular surface is broader and less clearly triangular, is inclined less strongly craniad, and is not so deeply concave. The slit into which the tendons of the M. biceps brachii and the M. brachialis insert is not as completely closed; seen ventrally the slit is a large irregularly triangular depression that is deepest proximally and is bordered by an anterior and a posterior ridge. The shaft is slightly thinner and is mostly round in cross section, but becomes progressively more anterioposteriorly compressed distally and is not flattened on its dorsal or ventral surface. The distal epiphysis is elongate dorsoventrally. The distal articular surface is bounded anteriorly by two low knobs and posteriorly by a broad low process. The ridge on the dorsal surface of the distal epiphysis is slightly larger and is not perforated. A small tubercle arises from the anteroventral rim of the articular surface. On the anterior surface of the radius are three ridges; the small

central ridge is bordered on each side first by a depression and then by a low ridge.

Macrotus.—The proximal epiphysis is broad and is inclined craniad to roughly the same degree as it is in *Eumops*. The depression in which the M. biceps brachii and the M. brachialis insert is not enclosed medially. The entire shaft is anteroposteriorly compressed and is flattened on neither the lateral nor medial surface. The distal epiphysis is elongate laterally and its articular surface is directed slightly caudad. The styloid process and anterior pseudostyloid process are represented by two small tubercles immediately inside the rim of the distal articular surface; the posterior pseudostyloid process is more strongly developed. In addition there is a well-developed process at the posteromedial rim of the articular surface. No ridge is present on the lateral surface of the distal epiphysis, but a stout process, which is in the same position as the distal end of the ridge in the other genera, forms a posterolateral extension of the articular surface. Two short, low ridges arise from the anteromedial rim of the distal articular surface. There are three ridges on the anterior surface of the distal epiphysis; they are similar to those in *Myotis* but are medial to the center of the anterior surface of the epiphysis.

Ulna

In *Eumops* the part of the ulna that lies against the proximal epiphysis of the radius is robust; the shaft of the ulna is thin, becomes threadlike distally, and terminates opposite roughly the middle of the radius. The body of the proximal part of the ulna is irregularly fusiform; the proximal end is truncate and the anterior surface is convex and smooth. The smooth surface fits in the shallow depression on the posterior surface of the proximal tip of the radius and extends slightly proximal to it. This small proximal extension of the ulna represents the olecranon process and on it inserts the M. triceps brachii. From the fusiform body of the ulna projects a broad, square-ended medial articular process. It is convex posteriorly and concave and smooth anteriorly and extends medial to the proximal tip of the radius where the medial articular process contacts the medial ridge of the trochlea.

Compared to *Eumops* the proximal part of the ulna is more symmetrical and less angular in *Myotis*. The articular surface of the body of the ulna is broader and slightly concave, and the medial articular process is smaller and does not extend as far mediad. The thin shaft ends within the proximal third of the forearm.

In *Macrotus* the articulation with the radius is less steady than in the other genera because the articulating surfaces are flat. The medial articular process is small and projects only slightly medial to the body of the ulna. The shaft is thin and fuses with the posterior surface of the radius approximately two-fifths of the way along the forearm.

Manus

A detailed description of each element of the manus is beyond the scope of this report. Nonetheless, a description of some of the more striking specializations and a discussion of their functional significance is worthwhile. A general idea of the carpi of the bats under consideration may be gained from figure 7.

Seemingly all the unique modifications evident in the bat's carpus serve the end of limiting movement of the wrist and digits to one plane. One of the basic prerequisites for efficient flight is the development of flight surfaces that can be held rigid against the force of the air stream. One way is which this rigidity is attained in bats is by limiting movement at the elbow, wrist and carpometacarpal joints (except the first) to the anteroposterior plane. The manus of bats has been rotated (supinated) 90 degrees from the position of the carpus in cursorial mammals; the digits are arranged one behind the other in the anteroposterior plane with the thumb foremost. When the digits are fully flexed they lie together next to the posterior surface of the radius. When the wing is completely extended the second and third digits project straight to the side and are nearly parallel with the distal part of the shaft of the radius; the fourth digit extends caudad at an angle of roughly 15 degrees to the third digit in *Eumops*. This angle varies considerably from one kind of bat to another; the angle is approximately 20 degrees in *Myotis* and 35 degrees in *Macrotus*. The fifth digit projects almost directly posteriad at an angle of roughly 90 degrees to the third digit.

The following descriptions are based on *Eumops* and indicate the types of specializations evident in the carpus. The lunar and cuneiform fit against each other and their rounded proximal surfaces fit into the deeply concave and laterally elongate distal articular surface of the radius. In the dorsal part of the anterior surface of the lunar is a broad groove along which the styloid process of the radius slides and a depression into which the process locks when the manus is fully extended. In the ventral part of the articular surface of the lunar is a second groove; this groove accommodates the anterior pseudostyloid process of the radius. In the posteroventral surface of the lunar is a broad groove bordered medially by a ridge. Along this groove moves the posterior pseudostyloid process of the radius. This system of tongue-in-groove articular surfaces limits movement at the radiocarpal joint to the anteroposterior plane, or when the wing is outstretched, to the horizontal plane.

The ventral surface of the carpus is spanned and reinforced by the pisiform. The bone is large and irregular in shape; its proximal end is attached by fascia to the ventral surface of the trapezium and its distal end is bound to the proximal part of the ventral surface of the fifth digit.

The proximal ends of all metacarpals except the first are modified so as to rest tightly against each other and brace each other. As additional strengthening the distal parts of some of the carpals are narrow and pointed and fit tightly between or against the proximal ends of the metacarpals. The dorsal part of the trapezoid is laterally compressed and pointed distally; it rests in a deep groove in the dorsal surface of the base of the second metacarpal and locks into a depression at the distal end of the groove when the metacarpal is fully extended. The dorsal part of the magnum is flattened on its posterior surface and lies closely against the flat proximal end of the third metacarpal; the distal edge of the ventral part of the magnum is narrow and fits in a space between the proximal ends of metacarpals two and three. Distally the unciform is divided into two lobes; the anterior lobe is thin and extends between the bases of metacarpals three and four. The flattened proximal end of metacarpal four extends into the depression between the two lobes of the unciform. The second and posterior lobe is bluntly pointed and

fits into an anteroposterior groove in the proximal end of the fifth metacarpal.

In *Myotis* and *Macrotus* the carpus is not so specialized as in *Eumops*, but in general the modifications are the same. The lunar is grooved, but the processes of the radius are not so well developed and the joint seems to be less strongly braced. The carpometacarpal joints are complex and although they differ in many morphological details from those in *Eumops* they achieve the same functional result.

The proximal ends of all metacarpals except the first in all three genera are highly specialized for strong articulations with the carpals and for movement in only the anteroposterior plane (Fig. 7). The digits are greatly elongated and are curved ventrad slightly giving the distal part of the wing horizontal camber. The metacarpals are the longest segments and the phalanges become shorter distally (except for the third digit in *Macrotus* in which the first phalanx is shorter than the second). The phalangeal formulae of the genera are as follows (the superscript "c" means that the distalmost phalanx is cartilaginous): *Eumops* and *Myotis*, 2-1-3^{c}-3^{c}-3^{c}; *Macrotus*, 2-1-3-3^{c}-3^{c}.

In all three genera the thumb is allowed free movement and is the only clawed digit. The phalanges are slightly laterally compressed and the claw strongly so. In all three genera the second digit is nearly round in cross section and terminates opposite the third metacarpophalangeal joint. In *Eumops* the end of the second digit is bound by connective tissue to the third metacarpophalangeal joint; the dactylopatagium minus is narrow and ends at this point. In *Myotis* and *Macrotus* the dactylopatagium minus is broad and ends at the joint between the first and second phalanges of the third digit. The third metacarpal is nearly round in cross section in *Myotis*, slightly dorsoventrally compressed in *Macrotus*, and considerably compressed in *Eumops*. The phalanges of this digit are round in *Myotis* and *Macrotus;* in *Eumops* the first phalanx is compressed and the second is round. The fourth digit is round in the three genera. The third and fourth digits of *Eumops* are remarkable for the direction of flexion of their phalanges. In *Myotis* and *Macrotus* these digits flex ventrally. In *Eumops*, in contrast, the first phalanges of the third and fourth digits flex posteriorly, and the second phalanges flex anteriorly. Due to this arrangement, when these digits are flexed the first phalanges lie along the distal parts of the posterior surfaces of the metacarpals and the second phalanges rest next to the anterior surfaces of the first phalanges. This accordionlike folding of the phalanges allows the long distal part of the wing to be folded into a bundle that does not project beyond the distal end of the third metacarpal. In all three genera the phalanges of the fifth digit flex ventrally, but are not allowed to flex as far as those of the other digits. This movement is most restricted in *Eumops*. The length of the fifth digit varies considerably; it is slightly shorter than the third metacarpal in *Eumops*, approximately 1.4 times as long in *Myotis*, and 1.6 times as long in *Macrotus*. The fifth metacarpal is interesting because of the specializations that strengthen the shaft of the metacarpal and reduce dorsoventral bending. Among the bats studied, the fifth metacarpal is most highly specialized in *Eumops*. In this genus the shaft is curved ventrad more abruptly than are the shafts of the other metacarpals. The proximal two thirds of the shaft is strongly laterally compressed and is broadest (dorsoventrally) at roughly the end of the first quarter; the greatest breadth of the

shaft is approximately 4.3 per cent of its length. As seen in cross section, the proximal two thirds of the shaft has a large, rounded dorsal part that blends into the central biconcave section; the ventral part is expanded slightly and is rounded ventrally (Fig. 7). In *Myotis* and *Macrotus* the shaft of the fifth metacarpal is laterally compressed, elliptical in cross section, and not nearly so robust as in *Eumops* (greatest breadth of shaft roughly 1.7 per cent its length in *Myotis*, 1.6 per cent its length in *Macrotus*).

Pelvic Girdle and Limb

Innominate Bone

Eumops.—This bone is heavily built and has strongly developed ridges and tuberosities. The pelvis is set on the sacrum at an angle; the dorsalmost part of the iliac crest is dorsal to the level of the neural spine of the first sacral vertebrae, whereas the center of the acetabulum is ventral to the level of the ventral surface of the centrum of this vertebra.

The ilium is tilted so that the gluteal fossa faces dorsad whereas the part of the ilium that is the dorsal rim in most mammals is directed mediad and contacts the sacrum. The sacroiliac joint involves that part of the thick medial portion of the ilium between the iliac crest and a point 2 mm. anterior to the acetabulum and the expanded lateral masses of the sacral vertebrae one to three. In adult individuals the ilium and the sacrum are solidly fused and the line of junction is difficult to trace. The anterior third of the ilium broadens abruptly and merges anteriorly with the broad, thick iliac crest. As seen anteriorly the ilium is roughly triangular; the most acute angle is represented by the iliac ridge that points laterad. The thickest part of the ilium is the medial part. The surface of the broad gluteal fossa is deeply concave; the ventral surface of the ilium faces ventrad and slightly laterad and is almost flat.

The acetabulum is large, faces dorsolaterad and somewhat caudad, and is situated immediately posterior to the middle of the innominate. Attached to the anterior cartilaginous rim of the acetabulum is a sesamoid bone from which the M. rectus femoris takes origin. The acetabulum is open posteroventrally.

The dorsal rim of the ischium is short and robust and at its posterior end the thick, rounded dorsal ischial tuberosity projects dorsad. The ascending ramus of the ischium is flat and moderately broad and is arched outward. The rami converge ventrally and from immediately anterior to the ventral ischial tuberosities bars of bone extend mediad and form a symphysis. I have available no skeletons of the bats here reported on that retain traces of sutures between the three bones that comprise the innominate bone. Probably the part of the innominate that surrounds the obturator fenestra and extends from the ventral rim of the acetabulum to the symphysis is the pubis; for descriptive purposes it will be so regarded. From the symphysis the pubis extends craniolaterad; the tip of the large pubic spine extends well anterior and slightly lateral to the acetabulum. The dorsal ramus of the pubis is broad and thick and from the ventral rim of the acetabulum is directed ventrolaterad. Probably due to the reptilian posture of the hind limbs in this bat, the pubes flare so sharply laterad as they extend forward from the symphysis that the width of the post-acetabular part of the pelvis as measured between the centers of the ventral borders is greater than the width between the dorsal borders. This is the reverse of the usual proportions in cursorial mammals.

Myotis.—The pelvic girdle of this genus is more lightly built and is not attached to the sacrum at so great an angle. The sacroiliac joint is not fused and involves only the first two sacral vertebrae. The lateral border of the ilium is straight and nearly parallel to the midline, or anteriorly converges slightly toward the midline in some specimens; the anterior end of the ilium is truncate and nearly round in cross section. The posterior two thirds of the ilium is roughly elliptical in cross section (the long axis is the lateral axis) and there is neither a gluteal nor an iliac fossa. There is a small tubercle immediately anterior to the acetabulum on which the M. rectus femoris originates. The dorsal ischial tuberosity projects more nearly caudad, and the ascending ramus angles more markedly caudad from the tuberosity. The ventral ischial tuberosity is larger. The symphysis is broader; the pubes extend less abruptly laterad and at a greater angle dorsad so that the post-acetabular part of the pelvis is not nearly so broad ventrally. The pubic spine is shorter and, in relation to the acetabulum, does not extend so far craniad or laterad. The dorsal ramus of the pubis is shorter and broader.

Macrotus.—In general the pelvis is more lightly built than those of the other two bats and is unusually small. The length of the pelvis is nearly the same in *Macrotus californicus* and *Myotis velifer* although the weight of the former bat is nearly twice that of the latter. The sacroiliac joint is not ankylosed and involves the first two sacral vertebrae. The ilium is rotated so far that the gluteal fossa faces dorsomediad and the iliac ridge points dorsolaterad. The anterior quarter of the ilium is expanded and is broader and thicker than the rest of the bone. There is a moderately well-developed gluteal fossa and a faint iliac fossa. A large sesamoid bone that gives origin to the M. rectus femoris is attached to the anterodorsal part of the cartilaginous rim of the acetabulum. The pelvis is narrow as measured across the bodies of the ischia; the ischia lie close to the lateral masses of the last sacral vertebrae and are connected to them by ligaments. The ascending ramus of the ischium is lightly built. The symphysis is narrow and the pubes are less widely spread apart than in *Eumops*, but, because the bodies of the ischia are so close together, the post-acetabular part of the pelvis is broader ventrally than dorsally. The pubic spine is extremely long, extending craniad beyond the level of the middle of the ilium. The dorsal rami of the pubes are longer than in *Myotis* and extend ventrolaterad from the ventral rim of the acetabulum.

Femur

Compared with the femora of most mammals those of bats are thin and long; also, they are long relative to the length of the shank.

Eumops.—The diameter of the shaft is approximately 4.7 per cent the length of the femur, and the femur is slightly longer than the shank. In cursorial mammals the head of the femur projects mediad from the proximal end of the bone; in this bat, however, the head angles craniad and only slightly mediad, being offset to the extent that the posterior surface of the head is approximately in line with the long axis of the shaft. The articular surface of the head extends around almost the entire head and the head projects well beyond the trochanters. These features suggest that a wide range of movements is possible at the hip joint.

The greater trochanter is broad, rounded distally, and extends proximolaterad from the short neck of the femur to a point opposite the middle of the head. The end of the greater trochanter bears two small marginal tubercles. A low, thin lateral ridge extends from the posterolateral surface of the greater trochanter onto the proximal part of the shaft. The lesser trochanter is slightly lower and narrower than the greater trochanter and gives rise distally to a low, broad medial ridge on which insert certain adductor muscles. The lesser trochanter projects proximomediad to roughly the level of the base of the head.

The shaft is nearly straight, but curves gently craniad and laterad. Roughly three fifths of the way along the lateral surface of the shaft is a short ridge to which the M. gluteus maximus and M. caudofemoralis attach.

The distal epiphysis is narrow (breadth of distal epiphysis approximately 2.3 times that of shaft) and extends posterior to the shaft a distance slightly less than the diameter of the shaft. The patellar groove is broader than either the lateral or medial condyle and the intercondylar fossa is deep. The center of the medial surface of the medial condyle is marked by a shallow pit, and the proximal part has a low prominence. The lateral condyle has at the center of its lateral surface a shallow depression. The articular surfaces extend around the posterior surfaces of the condyles to the point at which the condyles meet the posterior surface of the shaft. This placement of the articular surfaces suggests that the shank is normally held in a flexed position.

Myotis.—The femur is slightly less robust (diameter of shaft approximately 4.3 per cent length of femur) and is shorter than the shank. Both trochanters extend to a point roughly opposite the middle of the head. The lesser trochanter merges distally with a moderately high medial ridge; the lateral ridge is represented by an elongate prominence at the distal base of the greater trochanter. The shaft is straight. The distal epiphysis is slightly broader (breadth of distal epiphysis approximately 2.7 times that of shaft), is cleft by a deeper intercondyloid fossa, and extends posterior to the shaft of the femur a distance greater than its diameter. The patellar groove is less clearly defined and, relative to the condyles, is narrower.

Macrotus.—The femur is longer than the shank and is slenderer than in the other two genera (breadth of shaft approximately 3.6 per cent length of femur). The head extends more nearly proximad than in the other genera. The head in *Macrotus* lies slightly anterior and lateral to the long axis of the shaft of the femur. The trochanters are small and knoblike. The lesser trochanter extends proximad and posteromediad immediately beyond the middle of the head. The greater trochanter projects laterad and does not extend beyond the base of the head. The medial ridge of the femur is thin and high and arises from the medial surface of the proximal fifth of the femur, starting immediately distal to the medial base of the lesser trochanter. The lateral ridge extends for roughly 1 mm. along the lateral surface of the second fifth of the femur. Immediately beyond the level of the trochanters the shaft turns abruptly laterad and then slightly mediad throughout the rest of its length. The proximal epiphysis, therefore, makes an angle of roughly 160 degrees with the distal four fifths of the shaft. The distal epiphysis is narrow (breadth of distal epiphysis approximately twice that of shaft) and extends only slightly posterior to the distal part of the shaft. There is a prominent tubercle on the lateral surface of the lateral condyle.

Tibia and Fibula

Eumops.—The tibia is heavily built and is shorter than the femur. The proximal epiphysis is broad and extends posterior to the shaft. The proximal articular surface is at right angles to the long axis of the proximal half of the shaft and is bilobed; each lobe is marked by a broad, shallow, anteroposteriorly aligned groove that articulates with a femoral condyle. The lateral condyle of the tibia is larger than the medial condyle and extends farther beyond the corresponding adjacent surface of the shaft. The proximal quarter of the shaft is roughly circular in cross section. At the end of the proximal eighth of the posterior surface of the shaft the heavy tendon of the M. semimembranosus inserts on a broad, elongate, rough-surfaced tubercle. A broad ridge approximately 1.5 mm. long arises roughly one third of the way along the posterior surface of the femur. The tendon of insertion used in common by the Mm. gracilis and semitendinosus attaches on the rough top of the ridge. This ridge gives way distally to a lower, thinner ridge that extends slightly beyond the middle of the posterior surface of the shaft. The distal two thirds of the shaft is laterally compressed, roughly elliptical in cross section, and curved caudad. The anterior edge of the distal half of the shaft bears a narrow crest that reaches its greatest height three quarters of the way along the tibia and gives origin to part of the M. tensor plagiopatagii. The distal epiphysis is expanded and is elongate anteroposteriorly. The distal end and lateral surface of the medial malleolus articulate with the medial and ventral surfaces of the astragalus. The lateral part of the distal articular surface faces distad and articulates with the dorsomedial part of the proximal half of the astragalus. The tendon of the M. plantaris passes along a depression in the posteromedial surface of the distal epiphysis of the tibia.

The fibula is slender but complete in *Eumops.* As viewed posteriorly the bone forms a gentle S-shaped curve; the proximal part of the shaft curves mediad and the distal part laterad. The medial surface of the head of the fibula contacts the lateral surface of the lateral condyle of the fibula. The proximal end of the fibula rests against a small bone that articulates distally both with the fibula and the lateral condyle of the tibia and articulates medially with the lateral condyle of the femur. The distal epiphysis is large and its broad lateral malleolus articulates with the dorsolateral part of the proximal end of the astragalus. The posteromedial part of the distal articular surface articulates with the ventral part of the proximal end of the astragalus.

Myotis.—The tibia is more slender and longer than the femur. The lateral condyle is extended caudolaterad as a broad, bluntly pointed projection that serves to increase the area of the articular surface. Only a small elongate prominence on the posterior surface of the tibia immediately distal to the proximal epiphysis marks the point of insertion of the hamstring muscles. The shaft of the tibia is nearly round in cross section, becomes progressively narrower distally, and curves slightly mediad. The medial malleolus is short and narrow.

In this genus the fibula is thin and incomplete; it extends from the proximal end of the carpus to within approximately 2 mm. of the lateral projection of the lateral condyle. The distal end of the fibula is expanded and contacts the dorsolateral part of the proximal end of the astragalus.

Macrotus.—The tibia is slightly shorter than the femur and is considerably thinner than in the other two genera. The lateral condyle is extended laterad as a pointed process that turns sharply distad at its tip. A short ridge extends onto the shaft from the medial condyle. A broad, rough tubercle, which serves as the point of attachment for the hamstring muscles, arises from the posterior surface of the tibia immediately distal to the proximal epiphysis. Distal to this point, the shaft is slightly laterally compressed and has low crests along its anterior and posterior borders. The shaft becomes progressively narrower distally and curves gently caudad. The distal epiphysis is expanded, and inclined posteriad, and the articular surface faces distad and slightly laterad.

The fibula in *Macrotus* extends along roughly the distal half of the shank and is thinner than in the other genera. It becomes broader distally and articulates with the dorsolateral part of the head of the astragalus.

Pes

In general the feet of these bats are unspecialized. They retain the primitive mammalian phalangeal formula (2-3-3-3-3) and in all three genera the foot is short, amounting to roughly 25 per cent of the total length of the hind limb. Lateral as well as anteroposterior movement is possible at the ankle-joint. The major specializations of the pes are as follows: elongation of the astragalus and calcaneus; development of the calcar; lateral compression of the phalanges and claws; elongation of the first phalanx of the first digit thus making all the digits nearly equal in length.

Eumops.—The foot is broader and the individual bones are more massive in this bat than in the other genera. The astragalus is irregular in shape and is roughly two thirds as long as the calcaneus. The astragalus articulates proximally with the tibia and fibula and distally with the navicular and cuboid. The fibula articulates with the broad, rounded proximal surface of the astragalus and the tibia contacts the middle of the dorsomedial surface. The distal end of the astragalus is rounded and elongate dorsoventrally. The astragalus is not in exact alignment with the plane of movement of the knee-joint, but extends slightly mediad. Thus, when relaxed, the foot "toes" inward slightly. The tendons of the M. tibialis posterior and the M. flexor digitorum fibularis pass along the grooved ventral surface of the astragalus. Roughly one third of the way along its length the dorsomedial surface of the calcaneus contacts the ventrolateral surface of the proximal end of the astragalus. The dorsolateral surface of the distal end of the astragalus and the dorsomedial surface of the distal end of the calcaneus are also in contact, and these bones are bound together by connective tissue throughout most of their lengths. The distal part of the calcaneus is laterally compressed; the distal articular surface is deeply notched and fits against the cuboid. The partly ossified base of the calcar articulates with a large concavity in the lateral surface of the proximal half of the calcaneus. The calcar is circular in cross section, mostly cartilaginous, and approximately 27 mm. long. Its proximal end is pointed, laterally flattened, and notched. A hollow in the posterior surface of the base of the calcar accommodates the rounded lateral part of the proximal end of the calcaneus and allows the calcar to be drawn caudad, toward the posterior surface of the shank, when the bat is crawling. The calcar is pulled laterad

during flight by the M. depressor ossis styliformis and serves to spread the uropatagium and reinforce its lateral edge. The medial tarsal (see Hill, 1937: 100) is large and crescent-shaped and lies at right angles to the long axis of the tarsus. The medial end of this bone rests against the ventral surface of the internal cuneiform. The thick, fleshy pad of the ventral surface of the tarsus is attached to the medial tarsal; this bone probably serves to protect the ventromedial part of the tarsus when the bat is crawling. The distal surface of the medial tarsal gives origin to the M. abductor hallucis brevis. The remainder of the tarsal bones present no unusual features. The base of the fifth metatarsal is broad and dorsoventrally flattened; from its ventral surface arises the M. abductor digiti quinti. In digits two to five, the segments, arranged in order from longest to shortest, are: first phalanges, metatarsals, second phalanges, third phalanges. In the first digit the first phalanx is the longest element and the second phalanx, the shortest.

Myotis.—The foot of this bat is more lightly built, but the basic pattern of articulation between the bones closely resembles that in *Eumops*. The astragalus angles more sharply mediad and is rotated slightly laterad; hence, when relaxed, the foot turns inward more sharply and is slightly supinated. The astragalus and calcaneus are in closer contact with each other and less movement seems to be possible between them. The flat, entirely cartilaginous calcar is truncate proximally and articulates with the ventrolateral surface of the proximal end of the calcaneus. The calcar is roughly 14.5 mm. long. The medial tarsal is small. There is a round sesamoid on the ventral base of the fifth metatarsal. The base of this bone is flattened and broad, but not so much so as in *Eumops*. The segments of digits two to five in *Myotis* become progressively shorter distally. The first phalanx is the longest segment of the first digit and the second phalanx, the shortest.

Macrotus.—The astragalus and calcaneus are shorter relative to the lengths of the digits than in the other genera, but the scheme of articulation is the same. The tibia and fibula both articulate with the proximal end of the astragalus and this bone extends almost directly distad in line with the tibia. The round proximal articular surface faces proximodorsad and the truncate distal articular surface, distad and slightly ventrad. The foot is slightly extended when relaxed, while in the other genera the foot remains partly flexed when relaxed. In *Macrotus* the foot is slightly supinated when relaxed. The cartilaginous calcar is oval in cross section, has a simple truncate base, is roughly 10 mm. long, and articulates with the proximolateral surface of the proximal end of the calcaneus. The dorsal part of the distal third of the calcaneus is enlarged and has two grooves in its dorsal surface through which pass the tendons of the Mm., peroneus longus and brevis. The tendons of the Mm. tibialis posterior and flexor digitorum fibularis pass along the depression between the medial surface of the proximoventral part of the calcaneus and the ventral ridge on the proximal part of the astragalus. The medial tarsal is small and lies on the ventral surface of the internal cuneiform. From the base of the fifth metatarsal a fingerlike tubercle projects proximolaterad. The relative lengths of the digits are as in *Myotis*.

MYOLOGY

Introductory Remarks

In the arrangement of the muscles I have followed almost entirely the system used by Hill (1937). Rinker's arrangement (1954) has been followed for muscles not mentioned by Hill. These systems were employed primarily because they are convenient to use in a study of functional morphology.

In connection with specific anatomical points, only in a few cases are the conclusions of early workers given. My findings are occasionally in disagreement with those of early authors, but it would add little to discuss these points of difference. Errors made by early workers may well have been due to the lack of adequate optical equipment for use in dissecting.

Except with regard to the hand, descriptive terms are applied to the bats considered here as they are to other mammals (see page 44). In the following accounts the brief description given under the headings "origin" and "insertion" are based on *Eumops*. In instances where no description is given for a muscle in *Myotis* or *Macrotus* the reader is to assume that the muscle does not differ significantly from the corresponding muscle in *Eumops*. The innervations of most of the muscles are given in parentheses next to the names of the muscles. Where no innervation is given this means that it was not determined.

Muscles Unique to Bats

M. occipito-pollicalis

ORIGIN.—From lambdoidal crest just lateral to midline.

INSERTION.—Along distal part of anterior surface of second metacarpal.

REMARKS.—This muscle is similar in all three genera. The origin is fleshy and the belly of the muscle passes over the anterior surface of the shoulder, to which it is bound by connective tissue. Between the shoulder and thumb the muscle gives way to a tendon that passes along the anterior edge of the propatagium, ventral to the base of the first phalanx of the thumb, and along the membrane on the leading edge of the wing to insert on the distal part of the anterior edge of the second metacarpal. The manner in which the muscle is bound to the shoulder varies. In *Eumops* a slip of the M. clavodeltoideus is reflected outward and, instead of inserting on the pectoral ridge of the humerus, ends in a short flat tendon intersecting the distal part of the belly of the M. occipito-pollicalis. The slip is slightly more than 1 mm. wide, and its distal part normally lies in a depression immediately proximal to the insertion of the M. clavodeltoideus. Continuing from the distal end of the belly

of the M. occipito-pollicalis in *Eumops* is a heavy band of elastic cartilage that becomes tendinous near the carpus. In *Myotis* a small strand of connective tissue arises from the distal surface of the M. clavodeltoideus and intersects the occipito-pollicalis. In *Macrotus* a flat tendon extends to the muscle from a slight depression extending at right angles across the fibers of the pectoralis muscle 2 mm. short of its insertion on the humerus. Seemingly the depression is caused by the tautness of the band of fascia that gives rise to the tendon.

This muscle was given the name occipito-pollicalis by Kolenati (1857:9), and the name was adopted by Macalister (1872:129). The phylogenetic origin of the muscle was disputed by early workers. The muscle was found by Macalister (*loc. cit.*) to be innervated by the spinal accessory nerve, and for this and other reasons he concluded that the muscle was a derivative of the occipital part of the trapezius. I was unable to trace the innervation of the M. occipito-pollicalis. Because the distal part of the muscle continues beyond the thumb to the second metacarpal, the name occipito-pollicalis is not descriptively correct. Because of the long usage of the name, however, I am retaining it.

ACTION.—The muscle increases the area and camber of the plagiopatagium by pulling the propatagium craniad and ventrad. This action greatly improves the effectiveness of the air foil of the wing. Photographs of *Myotis* and *Macrotus* in flight demonstrate that in these genera, when the wing is fully extended, the propatagium is stretched taut between the shoulder and the base of the first phalanx of the thumb; the leading edge of the membrane curves only slightly posteriad. In *Eumops* the propatagium narrows rapidly toward the middle of the radius and even when fully spread the membrane curves sharply toward the elbow. The breadth of the propatagium has an important effect on the camber of the wing.

The placement of the origin of the tendon binding the belly of the M. occipito-pollicalis to the front of the shoulder seems to be correlated with the aerodynamic differences between the wings of the three genera. In *Eumops*, which has a high speed, narrow wing, low camber is achieved by the high placement of the origin of the binding tendon and the resulting shallow angle of the propatagium. In *Macrotus* the placement of the origin of the binding tendon is low—near the insertion of the M. pectoralis—and the propatagium is pulled sharply downward; this helps to produce a high-lift wing of high camber. Photographs of *Macrotus* in level flight show that when the wing is extended the propatagium is drawn downward at an angle of roughly forty degrees to the plagiopatagium. In *Myotis* the shoulder tendon originates on the M. clavodeltoideus, but not so high as in *Eumops*.

M. coraco-cutaneus

ORIGIN.—From posterior surface of distal part of medial ridge of humerus.

INSERTION.—Into plagiopatagium.

REMARKS.—In *Eumops* this muscle is relatively larger than in the other species. The long slender tendon of origin gives rise to a fusiform muscle bundle roughly 9 mm. long that extends posteriad and laterad into the proximal part of the plagiopatagium and terminates as a group of cords of elastic cartilage that pass into the network of elastic strands reinforcing the posterior

part of the plagiopatagium. In *Myotis* the origin is from the tip of the coracoid process. In *Macrotus* the muscle takes origin from the fascia on the dorsal surface of the belly of the coracoid head of the biceps.

ACTION.—This muscle helps reinforce the plagiopatagium by anchoring the supporting network of elastic fibers in this membrane to the axilla.

M. humeropatagialis

ORIGIN.—From fascia over medial epicondyle of humerus and posteromedial surface of ulna, and by thin fascial sheet from medial surface of humerus.

INSERTION.—Into the plagiopatagium.

REMARKS.—Of the genera under study, this muscle is present only in *Eumops*, in which it is cylindrical, approximately 20 mm. long and 1.5 mm. wide, and extends distad and slightly caudad into the plagiopatagium. The muscle was found in all the molossid bats that I examined. I have found no reference in the literature to this muscle, and describe it here under the new name Musculus humeropatagialis.

ACTION.—This muscle braces and tenses the anterodistal part of the plagiopatagium.

M. depressor ossis styliformis

ORIGIN.—From dorsolateral surface of calcaneus and dorsal part of base of fifth metatarsal.

INSERTION.—Along roughly 12 mm. of anterior surface of calcar.

REMARKS.—This muscle is approximately the same in all three genera, but is somewhat shorter in *Myotis* and *Macrotus* (roughly 6 mm. long in each). The name used here for this muscle was first proposed by Macalister (1872:159).

ACTION.—By pulling the calcar laterad this muscle spreads the uropatagium and keeps it taut.

M. tensor plagiopatagii (tibial nerve)

ORIGIN.—In two parts. First part from distal three quarters of medial surface and anterior crest of tibia and also from fascia on ventral surface of tarsus (a sheet becoming progressively thicker distally; when relaxed, fibers lie along medial surface of shank and extend proximad from their origin). Second part on medial surface of internal cuneiform and base of first metatarsal (band approximately 2.5 mm. wide at base and 10 mm. long) becoming narrower distally.

INSERTION.—First part into that part of plagiopatagium attaching to anterior surface of shank. Fibers extend approximately 6 mm. into membrane when plagiopatagium fully spread. Second part extending along trailing edge of plagiopatagium and merging with elastic connective tissue that reinforces posterior edge of plagiopatagium.

REMARKS.—Among the bats under discussion here, this muscle occurs only in *Eumops*, but in the Family Molossidae is present and varies but little in all species that I have examined. I find no mention in the literature of the muscle concerned and here propose for it the new name Musculus tensor plagiopatagii.

ACTION.—This muscle helps maintain the tautness of the posterior part of the plagiopatagium when the wings are spread. An equally important function

may be to strengthen the connection between the plagiopatagium and the lower leg, as the fast flight characteristic of many molossid bats demands strong, well-braced flight membranes.

Muscles of the Pectoral Girdle and Limb

Trapezius Group

M. acromiotrapezius and ***clavotrapezius*** (spinal accessory nerve)

ORIGIN.—Along mid-dorsal line from level of last cervical to fifth thoracic vertebra.

INSERTION.—On medial surface of distal end of clavicle, entire medial surface of acromion process, and rim of scapular spine.

REMARKS.—In all three genera the muscle becomes thicker anteriorly, and the anteriormost part, which originates on the first thoracic vertebra, is more or less separated from the rest of the muscle. The anteriormost part is probably a remnant of the clavotrapezius that has lost its cervical connections. In *Eumops* the anteriormost part is only indistinctly separated from the rest of the muscle, and the muscle fibers give way to a strong raphe, which is attached to the knoblike neural spine of the first thoracic vertebra. From this raphe large flattened tendons extend downward and laterad and attach to the dorsal surfaces of the transverse processes of the first thoracic vertebra. As a result an X is formed; the upper arms are the muscle fibers descending to the raphe, and the lower arms are the tendons passing ventrad and laterad to the first thoracic vertebra. Thus, an unusually strong origin for the anterior division of this muscle is created.

In *Myotis* the anterior part takes fibrous origin on the dorsal surface of the first thoracic vertebra. In *Macrotus* the origin closely resembles that in *Eumops*. The insertion is on the medial surface of the acromion and medial edge of the distal third of the clavicle, and the two parts of the muscle are more nearly separated than in the other two genera.

ACTION.—This muscle pulls the clavicle and scapula mediad and tips the vertebral border of the scapula downward. The remarkably strong origin of the anterior part of this muscle and the large size of the entire muscle suggest that it is important in steadying the clavicle and anterior part of the scapula, against the pull of the powerful ventral flight musculature. Because of its insertion on the prominent acromion process, this muscle is mechanically well situated to aid in the upstroke of the wing by steadying the medial edge of the scapula against the forces resulting from the contraction of the deltoid muscles.

M. spinotrapezius (spinal accessory nerve)

ORIGIN.—From the mid-dorsal line over thoracic vertbrae eight to thirteen.

INSERTION.—Along middle third of medial border of scapula adjacent to intersection of spine and medial border.

REMARKS.—In *Eumops* all but the fleshy anterior part of the origin is fibrous; the insertion is fibrous anteriorly becoming fleshy posteriorly. In the other two genera the origins and insertions appear fleshy.

In *Myotis* the origin is from thoracic vertebrae seven to ten. In *Macrotus* the muscle takes origin from thoracic vertebrae ten to thirteen and inserts along

the medial border of the scapula from a point immediately anterior to the junction of the spine and medial edge to a point slightly anterior to the posterior end.

ACTION.—This muscle pulls the scapula posteromediad and tips the medial edge ventrad, thus acting with the M. clavotrapezius and M. acromiotrapezius to brace the scapula against the pull of the ventral flight muscles.

Costo-spino-scapular Group

M. levator scapulae (dorsal scapular nerve)

ORIGIN.—By four large slips, from transverse processes of cervical vertebrae four to seven.

INSERTION.—Along vertebral border of scapula from posterior end of anteromedial flange to junction of spine and vertebral border of scapula.

REMARKS.—In *Myotis* the origin is from the transverse processes of cervical vertebrae three to six, by four slips. In *Macrotus* the origin is by three slips from the transverse processes of cervical vertebrae four to six.

ACTION.—This muscle pulls the anteromedial border of the scapula forward and ventrad; when the scapula is braced by other muscles, the M. levator scapulae lifts the head and neck. While a bat is in flight the scapulae rock back and forth on their long axes with each wing stroke. Intermittent contractions of this muscle, associated with bracing the scapulae, would necessitate reciprocal contractions of antagonistic muscles in order to steady the neck. It seems likely that this bracing action, at least in steady flight, is not this muscle's major function. Also it is difficult to see how this muscle would exert a steady enough pull to hold up the head and neck while the bat is in flight. Perhaps this muscle functions mainly to brace or move the scapula in sudden maneuvers demanding a departure from the standard wing stroke.

M. serratus anterior (dorsal scapular nerve)

Anterior Division

ORIGIN.—From broad band along middle sections of ribs one to four, by four slips.

INSERTION.—On anteromedial surface and rim of anteromedial flange of scapula.

REMARKS.—The origin in *Myotis* is by five slips that cover the distal end of the first rib and a 3 mm. wide band along the distal surfaces of ribs two to five. In *Macrotus*, the muscle originates on the first rib and costal cartilage.

ACTION.—This is the most effectively situated muscle to exert a direct ventral pull on the anteromedial edge of the scapula. Working with the trapezius group of muscles the anterior division of the M. serratus anterior anchors the medial edge of the scapula and may help initiate the upstroke of the wing.

Posterior Division (long thoracic nerve)

ORIGIN.—By eight heavy slips, from along distal surfaces of ribs one to eight. Area of origin widens from roughly 2 mm. anteriorly to 10 mm. posteriorly.

INSERTION.—Along posterior two thirds of axillary border of scapula, along adjacent lateral 3 mm. of M. subscapularis and lateral edge of M. infraspinatus

and on entire ventral surface and lateral half of dorsal surface of posterior cartilaginous extension of scapula.

REMARKS.—The band of origin in *Myotis* extends from the short, broad first costal cartilage, along the distal ends of ribs two to nine. The origin broadens posteriorly, extending along roughly 5 mm. of costal cartilages eight and nine. In *Macrotus* the origin extends from ribs two to 10, and is approximately 4 mm. wide posteriorly.

ACTION.—Second to the M. pectoralis the posterior division of the M. serratus anterior is the largest muscle in the bats under consideration. It is thick, divided into slips at its origin, and has a broad, fleshy insertion. In most mammals the M. serratus anterior inserts on the vertebral border of the scapula, but in bats the insertion is on the lateral border. Attending this difference in insertion is a change in function. The M. serratus anterior in cursorial mammals cradles the body between the scapulae and serves to bear much of the weight of the anterior part of the body. This function is no longer important to bats, as these animals use the forelimb primarily for flight and seldom for quadrupedal locomotion. In bats the posterior division of the serratus anterior is so situated as to be an efficient depressor of the axillary border of the scapula; this action serves directly in the downstroke (power stroke) of the wings.

It was mentioned in the description of the humerus that the greater tuberosity functions as a locking device to stop the upward stroke of the humerus when it has reached the angle to the scapula at which the greater tuberosity meets the scapula. At this locking point the force of the stroke is transmitted to the scapula, tending to rock the scapula by pulling the lateral border upward. Contraction of the posterior division of the serratus anterior at this point in the cycle would not only stop the tipping of the scapula but, by depressing the lateral border and thus starting to push the locked humerus downward, would initiate the downstroke without the help of the large adductors of the humerus. The scapula rotates slightly about its anteroposterior axis, and the connection between the clavicle and the scapula constitutes the single fairly rigid point along this axis. The elastic effect of the tonus of the large serratus muscle is probably sufficient to reduce greatly rocking of the scapula at the top of the upstroke and thus the upstroke is terminated. By manipulating preserved specimens of *Eumops* it was found that a full contraction of the posterior division of the serratus anterior would swing the humerus downward through an arc of at least twenty-five degrees. The labor of the downstroke, then, is divided between the powerful adductors of the humerus—the M. pectoralis and the M. subscapularis—and the posterior division of the M. serratus anterior. The control of the downstroke is probably as follows: at the peak of the upstroke, when the humerus locks against the scapula, the lateral edge of the scapula is anchored by the serratus anterior; the downstroke of the wing is started by the contraction of this muscle with the resulting depression of the lateral border of the scapula and the lowering of the humerus; the large adductor muscles then take over and pull the humerus through most of its downstroke. It should be stressed that the posterior division of the serratus anterior may act to move the wing only when the humerus is in its locked position. Perhaps the major importance of this muscle lies in its relieving the adductors of the job of stopping the upstroke of the wings and beginning the

downstroke, and of allowing the adductors to rest during the upstroke and while the upstroke is stopped and the downstroke is begun. For a major flight muscle this increase in the proportion of resting time to working time in the wing-beat cycle may be extremely important when the wings are beat rapidly.

M. rhomboideus (dorsal scapular nerves)

ORIGIN.—From dorsal surfaces of thoracic vertebrae one to seven.

INSERTION.—Along entire post-spinous part of medial border of scapula including posterior cartilaginous extension.

REMARKS.—The muscle takes origin in *Myotis* from thoracic vertebrae one to five. In *Macrotus* the origin is from thoracic vertebrae one to six; the insertion is relatively less extensive than in the other two genera because *Macrotus* lacks a posterior cartilaginous extension on the scapula.

ACTION.—This muscle pulls the scapula mediad and tips the vertebral border ventrad. Together with the trapezius muscles the M. rhomboideus braces the scapula and helps control the upstroke of the wing.

M. omocervicalis (third cervical nerve)

ORIGIN.—From short, posteroventral spine at base of transverse process of atlas.

INSERTION.—On tip of acromion process.

REMARKS.—In *Macrotus* the origin is from the ventral arch of the atlas and the insertion on the anterior surface of the middle of the clavicle.

ACTION.—In most mammals this muscle draws the scapula forward and mediad. In bats the scapula is powerfully braced by heavy muscles associated with flight and the M. omocervicalis probably serves to draw the head and neck caudad. In *Macrotus* the shift of the insertion to the clavicle may be associated with this bat's greater ability to move the head and neck.

Latissimus-subscapular Group

M. latissimus dorsi (subscapular nerves)

ORIGIN.—From mid-dorsal line over thoracic vertebrae ten to thirteen and on lumbodorsal fascia to level of fourth lumbar vertebra.

INSERTION.—By short, heavy tendon shared with M. teres major, on distal end of medial ridge of humerus

REMARKS.—This muscle has a fleshy origin and tendinous insertion in all three bats. The origin in *Myotis* is from thoracic vertebrae nine to eleven and on the first two lumbar vertebrae; the insertion is on the distal end of the medial ridge of the humerus slightly medial to the insertion of the M. teres major. In *Macrotus* the origin is from thoracic vertebrae ten to twelve and lumbar vertebrae one to four; the insertion is on the medial ridge of the humerus just proximal to the insertion of the M. teres major.

ACTION.—This broad, long muscle is a flexor and rotator of the humerus and can act upon the humerus nearly throughout its range of movement. Because of the rigid build of the elbow and wrist joints, allowing motion only in the anteroposterior plane, contraction of the M. latissimus dorsi tends to pronate the entire forelimb. The presence of the ventral ridge on the humerus increases the effectiveness of the M. latissimus dorsi and M. teres major as

pronators by moving the insertions of these muscles away from the long axis of the humerus. These muscles may act to control the rotational stability of the humerus during the upstroke of the wing by acting as counter rotators against the deltoideus muscles and the M. infraspinatus, and, in addition, in terrestrial locomotion, help in the propulsion part of the stride of the forelimb.

M. teres major (subscapular nerves)

ORIGIN.—From lateral third of posterolateral facet of scapula.

INSERTION.—By common tendon with M. latissimus dorsi on distal end of medial ridge of humerus.

REMARKS.—The entire posterolateral facet of the scapula is covered by the origin of this muscle in *Myotis;* the insertion is by a fibrous sheet on the distal end of the medial ridge of the humerus immediately lateral to the insertion of the M. latissimus dorsi. In *Macrotus* the origin is over the posterolateral facet of the scapula; the lateral fibers take origin from the dorsal surface of the expanded rim of the scapula, and the medial fibers originate from the surface of the M. infraspinatus. The insertion is by a broad flat tendon on the end of the medial ridge of the humerus distal to the insertion of the M. latissimus dorsi. The M. teres major in *Macrotus* is larger, relative to the latissimus dorsi, than in the other two genera.

ACTION.—The function of the M. teres major — rotation and flexion of the humerus—corresponds closely to that of the M. latissimus dorsi.

M. subscapularis (subscapular nerve)

ORIGIN.—From entire ventral surface of scapula, including posterolateral (inner) surface of anteromedial flange and ventral surface of posterior cartilaginous extension.

INSERTION.—On proximal part of lesser tuberosity of humerus.

REMARKS.—This is the third largest muscle in the bats under consideration, being only slightly smaller than the posterior division of the M. serratus anterior. Macalister stated (1872:143) that "probably the largest subscapulars in the animal kingdom are possessed by bats." Seemingly the large anteromedial flange of the scapula and the unusual faceting of the scapula are modifications to increase the area of origin of the large subscapularis. The muscle is composed of two thick, bipinnate parts, the fibers of each part inserting on a broad, central tendon. One tendon lies in the trough formed by the posterolateral and intermediate facets, and the other, in the trough formed by the anteromedial facet of the infraspinous fossa and the supraspinous fossa. The insertion is partly fleshy and partly by the extensions of the two heavy, tendinous partitions. Proportionally, this muscle is largest in *Eumops* and smallest in *Macrotus.* The lack of an anteromedial flange and cartilaginous extension on the scapula limits the area of origin of the M. subscapularis in *Macrotus;* otherwise, the attachments of this muscle seem not to differ in the three genera.

ACTION.—This muscle adducts and extends the humerus. The attachments of the muscle suggest that it has little mechanical advantage for power, but can produce rapid action. Large size of the M. subscapularis, and the osteological specializations associated with its origin, indicate that the muscle is important. Its action is approximately that produced by the common con-

traction of the anterior and posterior divisions of the M. pectoralis. The principal function of the subscapularis is clearly to work with these muscles and with the posterior division of the M. serratus anterior in producing the downstroke of the wings. In addition, the subscapularis helps to support the weight of the anterior part of the body in terrestrial locomotion by adducting the humeri.

Deltoid Group

M. clavodeltoideus (axillary nerve)

ORIGIN.—From distal quarter of ventral surface of clavicle.

INSERTION.—On dorsal edge of proximal half of pectoral ridge of humerus.

REMARKS.—In *Myotis* the origin is from roughly the distal third of the clavicle; the insertion is along the proximal two-thirds of the pectoral ridge and the anterior surface of the base of the greater tuberosity of the humerus. In *Macrotus* the insertion is along the dorsal edge of the proximal angle and end of the pectoral ridge. The origin is roughly the same as in *Myotis*.

The M. clavodeltoideus is clearly separated from the anterior division of the M. pectoralis only in *Macrotus*. Here the fibers of the muscles lie at different angles, and the medial border of the M. clavodeltoideus overlies the lateral border of the anterior division of the M. pectoralis. In the other two genera these muscles appear more or less continuous with one another and the exact division between them was not determined with certainty. A small branch of the axillary nerve crosses the dorsal surface of the humerus, passes between the proximal end of the pectoral ridge and anterior base of the greater tuberosity, and penetrates the ventral surface of the M. clavodeltoideus. By tracing this nerve into the muscle and finding where the adjacent M. pectoralis began being innervated by the anterior thoracic nerve it was possible to gain a rough idea of the relative extend of the M. clavodeltoideus and the anterior division of the M. pectoralis.

ACTION.—This muscle is an extensor of the humerus and probably works with the pectoralis muscles when the wing stroke is directed forward. The M. clavodeltoideus also serves in quadrupedal locomotion to extend the humerus at the start of the stride.

M. acromiodeltoideus (axillary nerve)

ORIGIN.—From lateral three-quarters of scapular spine and entire lateral surface of acromion process of scapula.

INSERTION.—On dorsal surface of pectoral ridge of humerus.

REMARKS.—This muscle in *Eumops* has a fleshy origin and thick fleshy insertion. In *Myotis* the fleshy origin is from the entire lateral surface of the acromion; the fibrous insertion is on the distal half of the dorsal surface of the pectoral ridge and along roughly one and one-half millimeters of the dorsal surface of the humerus adjacent to the distal end of the pectoral ridge. In *Macrotus* this muscle is divided into two parts; the first part takes origin on the expanded anterior end of the acromion process and inserts on the dorsal surface of the pectoral ridge; the second part originates along the entire acromion process posterior to the tip, and inserts along roughly 2 mm. of the dorsal surface of the humerus starting opposite the distal end of the pectoral ridge.

ACTION.—This muscle elevates and rotates the humerus, and with the M. spinodeltoideus controls the upstroke of the wing. It is difficult to estimate the power requirements of the upstroke of the wing in bats, but some understanding of the requirements can be gained by a comparison of the upstroke cycle of the wing-beat in bats and birds.

In most birds—not in swifts and hummingbirds (Savile, 1950)—the upstroke requires little power and creates little thrust or resistance (drag) relative to the down stroke. This economy of power during the upstroke is obtained largely by the partial closing of the wings and the spreading apart of the primary feathers to reduce air resistance, and by raising the wing with the leading edge uppermost so that the air stream and muscles cooperate in its elevation. Economy of power in the upstroke is achieved similarly in bats. In bats also the wing is elevated partly closed and with the leading edge uppermost. In contrast to birds, however, bats have continuous flight surfaces and consequently are unable to "feather" the distal segment of the wing as effectively as do birds. More drag is created, with a resultant demand for more power. Accordingly, the elevating muscles in bats are fairly large.

Photographs of *Macrotus* in level flight show that the humerus moves downward and forward during the downstroke, and is raised upward and backward during the upstroke. This latter action can be produced by the common action of the spinodeltoideus and acromiodeltoideus muscles, and it is these muscles that supply much of the power needed for the upstroke.

The slight differences between the connections of the spinodeltoideus and acromiodeltoideus muscles in the three genera of bats here considered may have considerable functional importance. In *Eumops* the placement of the origins of these muscles is such that they are posterior to the main axis of the humerus throughout its normal range of activity; the insertions are both on the dorsal surface of the pectoral ridge, anterior to the long axis of the humerus. Their contraction, together or singly, would result in a fairly limited range of movements, all acting to elevate and flex the humerus. *Eumops* forages in the open, and its rapid, enduring flight probably calls for wing strokes directed mainly in one plane, with relatively little need for a large variety of wing actions. The restriction of the upstroke to an up and back direction probably achieves an efficient concentration of power within this limited range of movement. In *Myotis*, while the placement of the origin of the M. acromiodeltoideus is roughly the same as in *Eumops*, the insertion is nearer the long axis of the humerus. Thus, in *Myotis*, the humerus can probably be pulled nearly straight upward. This bat forages near vegetation, and maneuverability, requiring wing strokes in a variety of planes, is needed. The greater freedom of movement possible in the upstroke may reflect this mode of flight. In *Macrotus* the M. acromiodeltoideus and M. spinodeltoideus are each divided into two parts, and each part has a separate origin and insertion. Seemingly these muscles can control a greater range of actions in *Macrotus* than in either of the other genera. *Macrotus* forages close to foliage or near the surface of the ground, and extreme maneuverability is of primary importance; the wings must be able to beat in many different planes at the expense of great efficiency in one plane.

M. spinodeltoideus (axillary nerve)

ORIGIN.—From medial quarter of spine and entire post-spinous portion of vertebral border of scapula including posterior cartilaginous extension.

INSERTION.—The muscle fibers aggregate distally and emerge with those of M. acromiodeltoideus, inserting on posterior border of M. acromiodeltoideus and on dorsal surface of pectoral ridge of humerus.

REMARKS.—In *Myotis* the origin is from the medial three-quarters of the top of the ligamentous spine of the scapula and the post-spinous part of the vertebral border of the scapula to the base of the posterior cartilaginous extension; the fibrous insertion is on the small knob in the middle of the lateral ridge of the humerus. In *Macrotus* the muscle is divided into two parts. The first part takes origin from the post-spinous part of the vertebral border and the posterior two thirds of the ligamentous extension of the spine of the scapula; the fibrous insertion is along roughly 2 mm. of the lateral ridge of the humerus opposite the middle of the pectoral ridge. The origin of the second part is from the anterior half of the ligamentous extension of the spine and the posterior half of the acromion process of the scapula; the fibrous insertion is on the lateral surface of the humerus at the distal base of the greater tuberosity. The posterior edge of the second part of the muscle is overlapped by the anterior edge of the first.

ACTION.—This muscle abducts (elevates) and flexes the humerus, and probably supplies most of the power, together with the M. acromiodeltoideus, for the upstroke of the wing. The spinodeltoideus is a strong rotator of the humerus in *Eumops*, and a less effective rotator in *Myotis* and *Macrotus*. Rotational stability of the humerus during the upstroke is probably controlled by the deltoideus muscles' working against the counter-rotational action of the Mm. latissimus dorsi and teres major.

This muscle is discussed more fully under the account of the M. acromiodeltoideus.

M. teres minor (axillary nerve)

ORIGIN.—From dorsolateral edge of scapula just posterior to glenoid fossa and from above middle of origin of long head of M. triceps brachii.

INSERTION.—On distal surface of greater tuberosity of humerus.

REMARKS.—This muscle is composed of a single, short, flat band of fibers. In *Myotis* it is especially thin and delicate. Otherwise, the muscle is similar in all three genera.

ACTION.—The muscle is a weak flexor and rotator of the humerus.

Suprascapular Group

M. supraspinatus (suprascapular nerve)

ORIGIN.—From entire supra-spinous fossa and medial surface of spine of scapula and from thick ligament that extends from anteromedial flange of scapula to tip of acromion and base of coracoid processes.

INSERTION.—On proximal part of lateral surface of greater tuberosity of humerus.

REMARKS.—The connections of this muscle are similar in all three genera. Relative to the other muscles taking origin on the scapula, M. supraspinatus is larger in *Macrotus* than in the other genera.

ACTION.—This muscle elevates, extends and rotates the humerus. This action is not part of the pattern of the usual wing-beat cycle, but is probably important in rapid turns and changes of level, or in alighting, when this action

helps raise the wings and draw them forward. When the humerus is at or above the horizontal, the structure of the humeroscapular articulation stops the humerus from being extended beyond a position in which it forms a right angle with the body in *Eumops;* the humerus may move slightly farther forward in *Myotis;* in *Macrotus* the greatest freedom is allowed, and the humerus may be extended forward much farther. The M. supraspinatus, therefore, can move the humerus forward to different degrees in the three genera. The far greater freedom of movement of the humerus and the larger size of this muscle in *Macrotus* seem to be associated with the remarkable maneuverability in flight of this bat. When *Eumops* and *Myotis* are walking this muscle helps extend the wing at the start of each stride, and in this action probably works together with the M. clavodeltoideus.

M. infraspinatus (suprascapular nerve)

ORIGIN.—From lateral surface of spine of scapula and all of infraspinous surface of scapula but lateral third of posterolateral facet.

INSERTION.—On distal part of lateral surface of greater tuberosity of humerus.

REMARKS.—In *Eumops* the muscle is composed of two bipinnate parts, the fibers of each part inserting on a broad, central aponeurosis. In *Myotis* the muscle is bipinnate, with a single aponeurosis; the muscle originates from all but the posterolateral facet of the infraspinous surface of the scapula and from the lateral surface of the spine and ligamentous extension of the spine of the scapula. The fleshy and fibrous insertion extends from the lateral surface to the distal base of the greater tuberosity of the humerus. In *Macrotus* the muscle is bipinnate, and the origin is from all of the infraspinous surface of the scapula except the rim of the posterolateral facet.

ACTION.—This muscle flexes, abducts, and rotates the humerus. It helps in the upstroke of the wing and in maintaining rotational stability of the humerus, its action being similar to that of the M. spinodeltoideus.

Triceps Group

M. triceps brachii, caput lateralis (radial nerve)

ORIGIN.—On posterolateral surface of humerus from level of distal base of greater tuberosity to level of distal end of pectoral ridge, and from entire concave, posterior surface of medial ridge and adjacent posterior surface of humerus.

INSERTION.—On the proximal end of the olecranon process.

REMARKS.—This muscle is similar in all three genera.

M. triceps brachii, caput medialis (radial nerve)

ORIGIN.—From distal three-quarters of posterior surface of humerus.

INSERTION.—On proximal end of olecranon process deep to tendons of long and lateral heads of triceps.

REMARKS.—In *Eumops* and *Myotis* this division of the triceps is distinct throughout its course from the other two divisions. In *Myotis* the muscle is thin and takes origin along the distal third of the humerus. In *Macrotus* the origin is on the medial ridge of the humerus just distal to the insertion of the teres major. The insertion is on the proximal end of the olecranon in all three genera.

M. triceps brachii, caput longus (radial nerve)

ORIGIN.—From axillary border of scapula along first 4 mm. posterior to glenoid fossa.

INSERTION.—On proximal end of olecranon process.

REMARKS.—The attachments of this muscle are similar in all three genera.

REMARKS ON THE TRICEPS GROUP.—Compared to the other divisions of the triceps, the medial head is small. The lateral head is large, indistinctly divided into a posterolateral portion and a posterior part, and fills the depression formed between the concave posterior surface of the medial ridge of the humerus, the posterior rim of the lesser tuberosity, and the posterior base of the head of the humerus. The long head is the largest division of the triceps, and is divided into a superficial and a deep portion. The origin of the long head is partly fleshy and partly by a fibrous sheet attaching to the tubercle immediately posterior to the glenoid fossa of the scapula.

In *Eumops* the tendons of the lateral head and the long head of the triceps converge distally and are bound together in a common sheath as they extend along the distal half of the humerus. Relative to the size of the animal, the medial head of the triceps is largest in *Eumops*. It is separate from the other divisions of the muscle, and gives rise, just short of the insertion on the ulna, to a large sesamoid bone in the depression on the posterior surface of the humerus between the prominent spinous process of the medial epicondyle and the capitulum. The sesamoid is attached to the ulna by a short, broad tendon. The tendons of the long head and lateral head of the triceps run through the deep groove on the posterior surface of this sesamoid bone. In *Myotis* the medial head is distinct from the other divisions of the triceps, and the tendon of the medial head enlarges into a thick cartilaginous pad over the posterior surface of the trochlea. A small sesamoid bone at the distal end of the pad is connected to the ulna by a short tendon. The tendons of the long head and lateral head of the triceps lie on the surface of this cartilaginous pad. In *Macrotus* the tendons of the three divisions of the triceps are bound together distally, and give rise to a single thick, padlike tendon over the posterior surface of the trochlea. The tendon connects directly to the proximal end of the ulna, and contains no sesamoid bone. Macalister (1872:146) incorrectly thought that in all bats a sesamoid bone occurs in the distal part of the triceps tendon.

ACTION.—The triceps group extends the forearm. The short olecranon process indicates that these muscles produce rapid but not powerful extension of the forearm. To achieve the maximum effect of thrust and lift from the wing-beat cycle, the M. triceps must extend the forearm rapidly at the start of the downstroke; as the downstroke continues the antagonistic biceps and triceps act to keep the wing rigidly outstretched. Toward the bottom of the downstroke the forearm is partly flexed, and remains in this posture until the start of the next downstroke. Because the long head of the triceps originates on the scapula posterior to the glenoid fossa, extension of the humerus by the major flight muscles during the downstroke tends to lengthen the distance between the origin and insertion of this muscle, thereby compensating for the shortening of the distance due to the extension of the forearm and proximal movement of the olecranon process. Thus, the long head of the triceps can act more effectively when the wing is extended than can the medial and

lateral heads, and is more important in steadying the forearm against the flexing action of the biceps than are the medial and lateral divisions. The triceps group is important also in quick manuevers calling for rapid extension of the wing.

Extensor Group of Forearm

M. extensor carpi radialis longus (radial nerve)

ORIGIN.—From low ridge extending from lateral epicondyle onto distal part of shaft of humerus.

INSERTION.—On dorsal base of first metacarpal and anterodorsal base of second metacarpal.

REMARKS.—In *Myotis* and *Macrotus* the fibrous origin is from the proximal edge of the lateral epicondyle of the humerus. The insertion is the same in all three genera. Relative to other forearm muscles, this is a large muscle. It is covered by a thick, glistening sheet of fascia. The fibers extend roughly one third of the way along the radius and give way to a heavy, flat tendon that passes beneath the tendon of the M. abductor pollicis longus and along a shallow groove in the anterior surface of the distal end of the radius. After passing beneath the transverse ligament, the tendon divides, and the two tendons extend beneath the tendon of the M. extensor pollicis brevis to their insertions. In *Eumops* the tendons of the M. extensor carpi radialis longus pass beneath the broad fibrous insertion of the M. extensor indicis.

ACTION.—This muscle acts directly to extend the first and second metacarpals and indirectly to extend the entire distal part of the wing. Function is discussed under the M. extensor carpi radialis brevis.

M. extensor carpi radialis brevis (radial nerve)

ORIGIN.—From distal part of ridge of lateral epicondyle of humerus.

INSERTION.—On anterodorsal surface of third metacarpal immediately distal to its base.

REMARKS.—In *Eumops* the fibrous origin is immediately distal to the origin of the M. extensor carpi radialis longus, and contains a large sesamoid bone in the depression immediately anterior to the lateral epicondylar ridge. The sesamoid bone has a concave articular facet that lies against the knob on the anterior edge of the proximal rim of the lateral epicondyle. The distal tendon of the M. extensor carpi radialis brevis contains a sesamoid bone just short of its insertion in all three genera. In *Myotis* the origin lacks a sesamoid bone, and is on the proximal edge of the lateral epicondyle immediately distal to the origin of the M. extensor carpi radialis longus. In *Macrotus* the origin of the M. extensor carpi radialis brevis lacks a sesamoid bone, and is in common with the smaller M. extensor carpi radialis longus. In all three genera these are the largest muscles in the forearm. Each muscle has a strong fascial covering, which becomes thick and glistening distally. The tendons are large and flat, and lie in shallow grooves in the anterior surface of the distal part of the radius.

ACTION.—This muscle acts directly to extend the third metacarpal, and indirectly to extend the distal part of the wing. Judging from their sizes and functions, this muscle and the M. extensor carpi radialis longus are the most important flight muscles in the forearm. Together they control the extension

of all the digits and the spreading of the distal half of the wing membrane. In terms of power requirements, this is the most demanding function of the forearm muscles. (In connection with the actions of these muscles, it should be stressed again that flexion and extension of all but the first digit in bats is in the anteroposterior plane; no other kind of movement of these digits can occur except by "give" at the joints or bending of the bones.) Because all of the digits but the first are connected by a membrane, the extension of the second or third fingers, which form the leading edge of the wing, will cause the extension of all the digits and the spreading of the distal part of the wing membrane.

The job of extending the distal part of the wing and holding it against the force of the air stream during each downstroke of a prolonged period of flight seems beyond the ability of these slender muscles. It is probable, however, that when the bat is in flight these muscles function as strong, non-elastic bands, that extend the distal half of the wing with relatively little muscular effort when the radius is extended. There seem to be two structural details that help these muscles accomplish this. The elasticity of the muscles is greatly reduced, both by their large tendons that extend to within roughly the proximal fourth of the muscles, and by the strong fascial sheets investing most of the bellies of the muscles. Because the origins of these muscles are proximal to the center of the lateral epicondyle of the humerus, extension of the radius tends to increase the distance between the origins and insertions of the radial extensors. The proximal displacement of the origins of these muscles, which is caused by the full extension of the radius, is considerable, and amounts to roughly 3 mm. in *Eumops*. Thus, assuming the muscles to be non-elastic, the extension of the radius would cause extension of the distal part of the wing by the pull directed from the proximally shifted origin, through the muscles, to the first three metacarpals. Strong contraction of these muscles would increase the speed of extension and rigidity of the distal part of the wing. A contraction of just sufficient strength to make the muscle react as a non-elastic cord, however, would cause extension of the distal part of the wing when the radius was extended. By this arrangement, then, part of the burden of extending the distal half of the wing is transferred to the extensor of the radius, the M. triceps brachii, and the slender radial extensors of the forearm are helped to perform their actions effectively and with a minimum of effort.

M. supinator (radial nerve)

ORIGIN.—From the depression in lateral epicondyle of humerus.

INSERTION.—Along first 10 mm. of anterolateral surface of radius.

REMARKS.—In all three genera this muscle originates by a large tendon that contains a sesamoid bone. The relationships of this short, broad muscle are similar in the three genera.

ACTION.—This muscle flexes the radius and braces the elbow joint.

M. extensor pollicis brevis (radial nerve)

ORIGIN.—From dorsal surface of proximal part of ulna and entire anterodorsal surface of slender shaft of ulna, and by fibers that attach to M. abductor pollicis longus and M. extensor indicis.

INSERTION.—On first metacarpophalangeal joint and on distal end of second phalanx of first digit.

REMARKS.—In *Eumops* the slender tendon divides into three parts over the carpus; the lateral two are bound to the sides of the first metacarpal, the middle tendon extends to the dorsal surface of the second phalanx. In *Myotis* and *Macrotus* the tendon is bound by fascia to the first metacarpophalangeal joint and then continues to its insertion on the second phalanx.

ACTION.—Extension of the thumb.

M. abductor pollicis longus (radial nerve)

ORIGIN.—Along all but first 10 mm. of proximal half of interosseous surface of radius.

INSERTION.—On scaphoid bone of carpus.

REMARKS.—The attachments of this muscle are approximately the same in all three genera. The tendon passes from the dorsal surface to the anterior surface of the radius roughly two thirds of the way along this bone. In *Eumops* a well-developed groove in the radius is present along the course of this tendon. In the other two genera the groove is not so clearly defined.

ACTION.—This muscle braces the ventral base of the fifth metacarpal. In most mammals the insertion is on the first metacarpal, and the muscle functions as an abductor of the thumb. In the bats under consideration here, the insertion is on the scaphoid, which lies on the anteroventral surface of the carpus, and the function of the muscle is completely different from that in most mammals.

When the bat is in flight, it is important aerodynamically that the fifth digit and hind limb hold the plagiopatagium at the proper angle of attack to develop lift. By reinforcing the fifth carpometacarpal joint, this muscle helps keep the joint from "giving" during the downstroke, and aids the fifth metacarpal in maintaining the plagiopatagium at the optimal angle. The action is exerted on the fifth metacarpal *via* the scaphoid and the pisiform bone. The distal end of the pisiform bone is strongly bound by fascia to the proximal part of the ventral surface of the shaft of the fifth metacarpal; the proximal end of the pisiform rests against the ventral surface of the trapezium, and is bound to the connective tissue of the ventral surface of the carpus. The distal end of the pisiform is solidly fixed, but the proximal end may move slightly. It is by anchoring the proximal end of the pisiform that the M. abductor pollicis longus steadies the fifth metacarpal. This muscle attaches to the anterior edge of the scaphoid, and this in turn is attached to the proximal end of the pisiform by a broad ligament. Accordingly, contraction of this muscle tends to move the scaphoid craniad, this pull being transmitted by the strong ligament to the proximal end of the pisiform. This bone is thus kept from being displaced caudad when the articulation between the carpus and fifth metacarpal is subjected to the strain caused by the force of the air pressure on the flight membranes and the fifth digit. If free dorsoventral movement were allowed at the articulation between the carpus and fifth metacarpal, the M. abductor pollicis longus would act as a ventral flexor of the fifth digit; but, because the joint allows little dorsoventral movement, this muscle serves instead to help the joint resist forces tending to cause dorsal extension of the fifth digit.

M. extensor digitorum communis (radial nerve)

ORIGIN.—By broad aponeurosis, from lateral epicondyle of humerus.

INSERTION.—By three tendons, on dorsal surfaces of distal ends of second phalanges of digits three, four and five.

REMARKS.—In *Myotis* the muscle gives rise to two tendons; the first divides into two parts over the carpus, one part inserting on the shaft of the first phalanx of the second digit, and the other on the distal end of the second phalanx of the third digit. The second tendon also divides; the large branch inserts on the shaft of the second phalanx of the fourth digit, and the small branch extends along the dorsal surface of the shaft of the fifth metacarpal where the tendon appears to join the tendon of the M. extensor digiti quinti proprius. The M. extensor digitorum communis has two partially separate bellies in *Macrotus*. One has a fibrous origin from the lateral epicondyle of the humerus and lateral surface of the proximal part of the ulna, and a fleshy origin from the posterodorsal border of the proximal half of the radius; the insertion is on the distal end of the third phalanx of the third digit. The second and smaller belly takes fibrous origin from the lateral epicondyle, and fleshy origin from the surface of the first belly; the tendon divides over the carpus, one division inserting on the distal end of the second phalanx of the fourth digit, and the other on the distal end of the second phalanx of the fifth digit. In *Macrotus* an extremely small tendon extends along the proximal part of the second metacarpal, inserting, in most specimens, at about the middle of the dorsal surface of the metacarpal. I found this tendon difficult to trace to its origin, but it appears to arise from the tendon of the division of the M. extensor digitorum communis, which inserts on the third digit. In all three genera the tendons of this muscle are bound by fascia to the digital joints across which the tendons extend.

ACTION.—This muscle extends the phalanges of digits three to five in *Eumops* and *Macrotus*, and the phalanges of digits two to five in *Myotis*, serving in each genus to spread the tip of the wing membrane. This is an important function, for the entire distal part of the wing is kept spread while the bat is in flight. Seemingly, however, the action demands little power; the muscle is long and slender and looks to be weak. Perhaps while the bat is in flight the air stream helps keep the wing membrane spread.

This muscle retains a functional connection with the second digit only in *Myotis* of the three bats considered. Because in the Microchiroptera the second digit is bound distally to the third digit and can not be extended separately, it would seem that an extensor of the phalanges of the second digit is unnecessary, and its loss in *Eumops*, and the great reduction in *Macrotus*, is what might be expected. Retention in microchiropteran bats of the part of the M. extensor digitorum communis serving the second digit, as seen in *Myotis*, is probably a primitive character.

M. extensor indicis (radial nerve)

ORIGIN.—Opposite middle half of forearm on posterodorsal surface of ulna and interosseus surface of radius.

INSERTION.—Mostly on dorsal base of second metacarpal.

REMARKS.—In *Eumops* the tendon spreads out over the dorsal surface of the carpus into a broad, fan-shaped aponeurosis and inserts on the anterodorsal surface of the carpus; the thickest part attaches to the dorsal base of the second digit. The origin in *Myotis* is from the distal tip of the ulna and the middle fifth of the interosseus surface of the radius; the insertion is by a thick tendon on the dorsal surface of the second metacarpal about 3 mm. from the base. In *Macrotus* the origin is along roughly the distal two thirds of the posterior surface of the radius; the insertion is by a large tendon on the dorsal base of the second metacarpal.

ACTION.—This muscle extends the second digit, thus helping the radial extensors to spread the distal part of the wing and steady its leading edge.

M. extensor digiti quinti proprius (radial nerve)

REMARKS.—I failed to find this muscle in *Eumops*. In *Myotis* the muscle arises by fibrous origin from the posterodorsal base of the ulna and by fleshy origin from the posterior edge of the M. extensor digitorum communis opposite the proximal third of the forearm; the insertion is by tendon on the dorsal surface of the shaft of the second phalanx of the fifth digit. This tendon is joined, over the fifth metacarpal, by a small tendon from the M. extensor digitorium communis. In *Macrotus* the M. extensor digiti quinti proprius takes fibrous origin from the proximal 3 mm. of the dorsal surface of the ulna and from the lateral epicondyle of the humerus; the insertion is on the dorsal surface of the tip of the second phalanx of the fifth digit.

ACTION.—In *Myotis* and *Macrotus* this muscle extends the fifth digit.

M. extensor carpi ulnaris (radial nerve)

ORIGIN.—Along first 8 mm. of posterior surface of ulna, and on distal half of posterodorsal surface of radius, by fleshy attachments.

INSERTION.—By large, broad tendon, on anteromedial base of third metacarpal.

REMARKS.—In *Eumops* the tendon extends proximad through much of the belly of the muscle, which is nearly the length of the humerus. Distally, the tendon becomes flat and broad, and passes beneath the tendons of the M. extensor digitorum communis to the third metacarpal. In *Myotis* the muscle originates by fascia from the posterior and dorsal surfaces of the base of the ulna, and fleshily from all but the first 3 mm. of the posterior surface of the ulna and the posterodorsal surface of the middle of the radius. The insertion is the same as that in *Eumops*. In *Myotis* the belly of the muscle extends along roughly the proximal three quarters of the forearm. The muscle is relatively smaller in *Macrotus* than in the other two genera, and inserts on the dorsal base of the fifth metacarpal as in most mammals. The origin is along the dorsum of the distal half of the ulna and the posterodorsal surface of the distal half of the radius.

ACTION.—In *Macrotus* the fifth digit is extended by this muscle. In *Eumops* and *Myotis* it is a powerful flexor of the third digit, and consequently of the entire distal part of the wing, and its action is directly antagonistic to that of the radial extensors.

In *Eumops* and *Myotis* the tendon passes over the posterior ridge on the distal end of the radius, along the edge of the carpus posterior to the third osteofibrous canal, and over the dorsal bases of metacarpals four and five to

its insertion on the base of the third metacarpal. The tendon passes posterior to the cuneiform bone, and is held there by a heavy fascial sheet. Because the tendon approaches the third digit from the posterior edge of the carpus, the tendon serves as an effective posterior flexor of the third digit.

It has been mentioned that when the radius is extended the distal part of the wing tends to be spread by the M. extensor carpi radialis longus and the M. extensor carpi radialis brevis. When the bat is using its wings for terrestrial locomotion the radius must be partially extended during the forward component of the stride, but the distal part of the wing must not be allowed to extend and must remain tightly closed. The principal function of the M. extensor carpi ulnaris is probably to act against the radial extensors and keep the distal part of the wing fully flexed during terrestrial locomotion. It is interesting that, among the bats here considered, only in *Macrotus*, which almost never uses its wings in terrestrial locomotion, does this muscle retain its insertion on the fifth metacarpal.

Pectoralis Group

M. subclavius (subclavius nerve)

ORIGIN.—From flat, ventral surface of first costal cartilage.

INSERTION.—Along all but distal quarter of posterodorsal edge and posterior third of flat, dorsal surface of clavicle.

REMARKS.—In *Myotis* this muscle takes fibrous origin from the anterior part of the distal base of the first rib; the insertion is along the middle two-thirds of the posterodorsal surface of the clavicle. In *Macrotus* the origin is as in *Eumops;* the insertion is along the middle three-quarters of the posterodorsal surface of the clavicle.

ACTION.—This muscle pulls the clavicle posteriad and ventrad, and probably serves mainly to steady the clavicle against forces pulling its distal ends together and forward.

M. pectoralis

This is a large, thick sheet of muscle that seems, superficially, to be undivided from the posterior end of the sternum to the shoulder. Actually, the muscle is composed of two major divisions, one taking origin from the clavicle and the other from the sternum. This division is present in all three genera. Macalister (1872:135) distinguished between the pars sternalis and the pars clavicularis of the pectoralis major in bats. Howell has concluded (1937:457) that "there is no ready criterion for distinguishing pectoralis minor from major elements." Lacking a means for assigning the two divisions of the large pectoral muscle to either the major or minor elements, I am referring to them as anterior and posterior divisions.

M. pectoralis, anterior division (anterior thoracic nerve)

ORIGIN.—From lateral surface of base, and all but distal quarter of flat, ventral surface of clavicle.

INSERTION.—By fibrous sheet, along dorsal edge of pectoral ridge.

REMARKS.—In *Myotis* the origin extends onto the manubrium and the muscle itself is divided into three parts in some individuals, but the completeness of the separations and the origins of the parts varies considerably. In all specimens that I have examined the deep division is more or less separate

and usually originates as a flat fleshy sheet on the ventral surface of the first costal cartilage and along the posterior border of the proximal two thirds of the clavicle; the insertion is by an aponeurosis along 1 mm. of the dorsal surface of the base of the pectoral ridge. The rest of the anterior division is sometimes separable into two parts: one takes origin from the manubrium and from the ligament that extends from the body to the spine of the manubrium, and inserts on the distal two thirds of the pectoral ridge; the other originates along roughly the proximal half of the ventral surface of the clavicle, and inserts on the dorsal edge of the proximal third of the pectoral ridge. In *Macrotus* the muscle is not divided, and originates from all but the distal 4 mm. of the ventral surface and edges of the clavicle. The insertion is on the proximal angle of the pectoral ridge.

ACTION.—This element of the pectoralis muscle pulls the humerus downward and forward and rotates it so that the leading edge of the wing is lowered.

M. pectoralis, posterior division (anterior thoracic nerve)

ORIGIN.—From ventral and lateral aspects of spine and entire ventral surface of the body of manubrium, ventral ridge of sternum and mid-ventral raphe to within 9 mm. of cartilaginous tip of xiphisternum, and from band extending 5 mm. laterally over seventh costal cartilage.

INSERTION.—On entire anterior surface of pectoral ridge, by heavy fibrous sheet.

REMARKS.—In *Myotis* the origin is from the ventral surface of the posterior end of the manubrium, the entire sternum and mid-ventral raphe to within 1 mm. of the cartilaginous tip of the xiphisternum, and from a 3 mm.-wide band extending laterally from the bony part of the xiphisternum along the abdominal fascia. In *Macrotus* the origin extends onto the manubrium and to within 2 mm. of the bifurcate tip of the xiphisternum, thence laterad on the abdominal fascia for roughly 5 mm.

ACTION.—The pectoralis muscle is a powerful adductor and rotator of the humerus and considering the anterior and posterior divisions together is easily the largest muscle in the bat's body. This muscle supplies the majority of the power for the downstroke of the wings. In *Eumops* the pectoralis muscle is approximately four times as heavy as the next largest muscle, the posterior division of the serratus anterior. Because the fibers of the pectoralis muscle originate from the xiphisternum to near the distal end of the clavicle, the muscle can govern adduction movements of the humerus through a wide range of planes. The anterior division draws the humerus downward and sharply forward, whereas the posterior part of the muscle pulls that bone downward and backward. The direction of the downstroke can thus be varied considerably by the pectoralis muscle alone. Seemingly the anterior and posterior divisions usually work together to produce the downstroke. By this common action the humerus is extended well forward, increasing the surface area of the wing to its maximum during the downstroke.

The large pectoral ridge on the humerus of bats puts the insertion of the pectoralis muscle well anterior to the long axis of this bone. Thus, this muscle acts as a rotator of the humerus, and, because of the rigidity of the elbow and wrist, tends to rotate the leading edge of the wing downward during the downstroke. This rotation is important aerodynamically. In birds the forward

propulsion for flight is supplied mostly during the downstroke when the distal primary wing feathers twist in response to the air pressure, each functioning as a propeller. The lift is supplied largely by the secondary feathers which remain at a relatively constant angle of attack throughout the cycle of the wing-stroke. These two main forces, forward thrust and lift, are produced similarly by the bat wing. The distal part of the wing forms a propeller, with the pitch increasing distally from the level of the last digit. Although the digits may "give" slightly dorsoventrally, the bat carpus allows only flexion and extension in the anteroposterior plane. In order to adjust the angle of attack of the wing, therefore, the humerus must be rotated. Only the fourth digit supports the trailing edge of the wing distal to the fifth digit; the second and third digits form the leading edge of the wing. The fifth digit aids the hind limb in maintaining the proper angle of the plagiopatagium throughout the downstroke. Therefore, during the downstroke, while the trailing edge of the distal part of the wing is tilted upward and is supplying forward propulsion, the fifth digit and the trailing edge of the plagiopatagium must be held down to maintain the camber and angle of attack necessary for developing lift. In other words, the fifth digit must be held at a different angle from the fourth digit during the downstroke. Interestingly enough, the fifth digit is modified in several ways in order, seemingly, to meet this requirement. Compared to the fourth digit, the shaft of the fifth metacarpal is curved more strongly downward, and the phalanges are slightly more flexed when the wing is spread. In addition, the fifth metacarpal is heavier and is laterally compressed. When not affected by air pressures, the trailing edge of the plagiopatagium is slightly lower than the trailing edge of the distal segment of the wing. Under the force of the downstroke this effect is magnified due to the greater flexibility of the fourth metacarpal and its more distal position in the wing subjecting it to greater air pressures. Photographs of bats in flight show clearly the twisting of the distal part of the wing during the downstroke. Probably, then, the tendency of the pectoralis muscle to rotate the humerus gives the plagiopatagium an advantageous angle of attack, in terms of lift, and it puts the fourth digit at an angle from which it may bend slightly and allow the distal segment of the wing to act as a propeller and supply forward thrust. The M. pectoralis also controls rotational stability of the wing during the downstroke by acting against the M. biceps brachii (pages 89-90).

The pectoralis muscles are important also in quadrupedal locomation in bats. The wings remain folded and the limb more or less flexed while the bat is walking or running, and the humerus is not vertical to the ground but is splayed out laterally. Accordingly, the pectoralis muscles must partly support the weight of the front part of the body by adducting the humerus. When the body is supported on the non-vertical forelimbs, part of the stride requires a downward and backward push; this movement is controlled largely by the pectoralis muscles. Thus, these muscles furnish a large share of the power necessary for both terrestrial and aerial locomotion.

M. pectoralis abdominalis (anterior thoracic nerve)

ORIGIN.—From abdominal fascia along strip roughly 9 mm. long and extending from 8 mm. lateral to midline, at level of base of xiphisternum, obliquely posteriad to approximately 15 mm. lateral to midline, at level of tip of xiphisternum.

INSERTION.—Along middle half of ventral edge of pectoral ridge, by thin aponeurosis.

REMARKS.—This is a long flat muscle underlying the posterior division of the pectoralis muscle. In *Macrotus* the insertion extends from the pectoral ridge onto the anterior surface of the base of the greater tuberosity of the humerus. Otherwise the relationships of the muscle are similar in all three genera.

ACTION.—This muscle is so situated as to be a strong flexor of the humerus, and also pulls it slightly downward. The primary function of this muscle is probably in connection with quadrupedal locomotion, for here this action produces the propulsion stroke for the front limb. Because of its length, this muscle can act on the humerus throughout a wide arc, and can fully flex it. Except in maneuvers demanding deviations from the usual wing-stroke cycle, this muscle is probably not important in flight.

Flexor Group of Arm

M. coracobrachialis (musculocutaneous nerve)

REMARKS.—This muscle is absent in *Eumops*. The fibrous origin in *Myotis* is from the lateral surface of the tip of the coracoid; the fleshy insertion extends along roughly 1 mm. of the medial surface of the humerus adjacent to the distal end of the medial ridge. In *Macrotus* the muscle takes fleshy origin from the dorsal edge of the tip of the coracoid process; the insertion is by a thin fibrous sheet on the medial surface of the humerus approximately 5 mm. beyond the distal end of the medial ridge. The coracobrachialis is smaller than either of the heads of the biceps in these genera.

ACTION.—This muscle is an adductor and extensor of the humerus. It probably helps the larger flight muscles depress the humerus; because of its small size, however, the coracobrachialis can be only a weak adductor. The coracoid head of the biceps seems to have taken over the function of the coracobrachialis in *Eumops*.

M. biceps brachii (musculocutaneous nerve)

ORIGIN.—Short head (coracoid head): from entire expanded tip, and all but medial surface of distal half of coracoid process of scapula, by thick, fleshy attachment. Long head (glenoid head): from lateral base of coracoid process of scapula, adjacent to anterior lip of glenoid fossa, by broad, thick tendon.

INSERTION.—Into deep slit in anteromedial surface of radius just distal to head.

REMARKS.—Because of the variations in the morphology of the scapula among bats, it is difficult to apply the standard terminology to the biceps muscles of these animals. The coracoid process turns strongly laterad in *Macrotus*, gently laterad in *Myotis*, but swings sharply mediad in *Eumops*. Accordingly, considering total lengths of muscles and tendons, the long head of the biceps is longer than the short head in *Macrotus*, roughly the same length as the short head in *Myotis*, whereas in *Eumops* the long head is actually shorter than the short head. Because of this possible source of confusion, it seems preferable to refer to the long head of the biceps as the glenoid head, and the short head as the coracoid head in the following remarks.

In *Eumops* the glenoid head of the biceps divides into two bellies as it passes through the bicipital groove. Each belly gives way to a broad, thick tendon roughly half way along the humerus; these tendons are separate to their insertions although bound in a common fascial sheath. The coracoid head of the biceps has a thick, fleshy origin; the belly gives way to a tendon approximately one third of the way along the humerus. The heavy tendon is bound in a fibrous sheath along with the tendons of the glenoid head, but remains a separate tendon. In terms of volume, the coracoid head of the biceps is larger than the glenoid head.

In *Myotis* the coracoid head of the biceps originates along the distal fourth of the coracoid process, and becomes tendinous one quarter of the way along the humerus. The coracoid head has roughly the same volume as the glenoid head. The large tendons of the biceps insert in a groove on the ventral surface of the radius immediately distal to the head of the humerus.

The coracoid head of the biceps takes origin in *Macrotus* from the enlarged distal end of the coracoid, and the tendon fuses with the broad, flat tendon of the glenoid head on the ventral surface of the latter. In contrast to the other two genera, the coracoid head of the biceps is smaller than is the glenoid head in *Macrotus*. The tendons of the biceps insert in a depression on the ventral surface of the radius immediately distal to its head.

ACTION.—These muscles are flexors and rotators of the forearm, and adductors of the wing. They are important in holding the forearm rigidly outstretched against the opposing forces of the triceps. Photographs of *Macrotus* in level flight, and in various stages of performing the half roll preparatory to alighting, show that the biceps muscles are in a state of contraction throughout much of the downstroke; in bats with wings almost fully spread the biceps tendons are pulled well away from the anterior edge of the humerus and appear as taut cords extending from the front of the shoulder to the proximal part of the radius. During the downstroke, for the sake of aerodynamic efficiency, the wings must be held stiffly extended against the force of drag created by the air stream. This steadying of the wing during the power stroke appears to be an important action of both the M. biceps brachii and the M. triceps brachii.

Throughout the upstroke the wing is partly flexed. This flexing, however, is probably passive. Compared with the position of the insertion of the triceps muscles, the position of insertion of the biceps tendons gives these muscles much greater mechanical advantage; therefore, under the control of the tonus of the biceps and triceps the forearm tends to flex.

The insertion of the tendons of the biceps is ventral to the long axis of the radius in all three genera. Thus, the biceps group acts to rotate the radius, tilting the leading edge of the wing upward, or, considering the action aerodynamically, increasing the angle of attack of the wing. This action also is associated with stabilizing the wing during the downstroke. The pectoralis muscles tend to rotate the humerus as they adduct it, their action being to lower the leading edge of the wing and decrease the angle of attack. Because of the rigidity of the elbow and wrist in bats, rotation of the brachium or antebrachium affects the entire wing. The rotating action of the biceps is in opposition to the rotating action of the pectoralis muscles. Probably the biceps muscles not only maintain the anteroposterior rigidity of the forearm by acting against the

triceps, but help control the rotational stability of the wing by acting as a counter-rotator against the action of the pectoralis. Expressed in terms of aerodynamics, the angle of attack during the downstroke may be the result of the antagonistic action of the biceps and pectoralis muscles.

The coracoid head of the biceps is clearly a more important muscle in *Eumops* than in either of the other two genera, and more effectively aids in the downstroke of the wing. It should be stressed prefatory to the following remarks that the long coracoid process enables the coracoid head of the biceps to act as an adductor of the humerus by placing its origin below the line of the long axis of the humerus, and that the greater this displacement, the greater the mechanical advantage of this muscle as an adductor. The medially curved coracoid process in *Eumops* takes the origin of the coracoid head of the biceps out of the way of the lesser tuberosity of the humerus, allowing more space for the origin and large belly of the muscle. In addition, the total length of the muscle and tendon is increased. Probably due primarily to the modifications in the coracoid process, the coracoid head of the biceps is relatively larger in *Eumops* than either of the other genera. Attending the other changes in *Eumops,* the function of the muscle is altered. In *Myotis* and *Macrotus* because of the laterally curved coracoid process, the origin of the coracoid head of the biceps is below the line of the long axis of the humerus when the wing is at the top of the upstroke, and in this position the muscle is effective as an adductor of the wing. The greatest mechanical advantage of the muscle as a brachial adductor is attained as the humerus reaches the horizontal, for here the origin of the muscle is at its maximum displacement from the line of the long axis of the humerus. The mechanical advantage of the muscle as an adductor is reduced, however, as the wing is fully depressed because the origin of the coracoid head of the biceps is no longer so far below the long axis of the humerus. Also, because of the relatively shorter length of this muscle in *Myotis* and *Macrotus,* it probably is not effective when the distance between its origin and insertion is shortened near the bottom of the downstroke. In short, the adduction action of the coracoid head of the biceps in these genera is effective at the top of the upstroke, reaches its peak efficiency when the wing is horizontal, and is reduced when the wing is depressed. In *Eumops,* in contrast, the origin of the muscle is only slightly below the line of the long axis of the humerus at the top of the upstroke because the humerus and the medially curved coracoid are nearly in line. At this point, then, the muscle is probably not effective as an adductor. The position of the origin of this muscle in relation to the line of the long axis of the humerus is lowered continuously through the downstroke of the wing, however, and the mechanical advantage of the muscle as an adductor is thus increased continuously throughout the downstroke. In *Eumops,* because of the medial curvature of the coracoid process, the distance between the origin and the insertion of the coracoid head of the M. biceps is probably always great enough for the muscle to function. Therefore, in *Eumops,* the coracoid head of the biceps serves most effectively as an adductor of the wing in the lower part of the downstroke. The modifications enabling the coracoid head of the biceps to help in the adduction of the forelimb seem to constitute an additional refinement in the system, characteristic of bats, of dividing the work of the powerstroke of the wing between a number of muscles.

M. brachialis (musculocutaneous nerve)

ORIGIN.—Along anterior surface of humerus from distal end of pectoral ridge to within roughly 5 mm. of distal end of humerus.

INSERTION.—Into deep slit in anteromedial surface of radius just distal to head.

REMARKS.—In *Myotis* and *Macrotus* the origin is from the third quarter of the anterior surface of the humerus. In all three genera the insertion of this muscle is the same as the insertion of the biceps muscles. This small muscle is relatively more robust in *Eumops* than in the other genera.

ACTION.—This muscle is a flexor and rotator of the radius, and probably acts with the biceps muscles to stabilize the wing during the downstroke.

Flexor Group of Forearm

M. flexor carpi ulnaris (ulnar nerve)

ORIGIN.—By large tendon, from tip of spinous process of medial epicondyle.

INSERTION.—On proximal end of pisiform.

REMARKS.—In *Eumops* the tendon of origin is 6 mm. long. The belly of the muscle is thin and flat, and lies along roughly the proximal two thirds of the forearm. The elasticity of the muscle is reduced by glistening fascial sheets that extend from the large tendons of origin and insertion and envelop most of the belly. A tendinous core passes through the belly of the muscle in *Myotis*. Otherwise, the muscle is the same as that in *Eumops*. In *Macrotus* the fleshy origin is from the anterior surface of the base of the ulna, the medial surface of the ulna, and by a thin sheet of muscle fibers along the distal part of the posterior border of the radius to within roughly 8 mm. of its distal end. The insertion is by a thin tendon on the proximal end of the pisiform.

ACTION.—This muscle is a posterior flexor of the fifth metacarpal. Because it is attached firmly to the ventral base of the fifth metacarpal, the pisiform serves as a proximal and ventral extension of the base of this bone. Thus, in terms of effect, when this muscle acts upon the pisiform, it is acting upon the fifth metacarpal.

In *Eumops* and *Myotis* two anatomical modifications seem to enable this muscle to control the degree of extension or flexion of the fifth metacarpal with little muscular effort. Because of the long spinous process of the medial epicondyle in these genera the origin of the M. flexor carpi ulnaris is moved through a wide arc when the radius is extended or flexed. In *Eumops*, for example, the origin of this muscle is moved 4 mm. proximad when the radius is moved from its position of maximum flexion to maximum extension. In contrast, due to its ulnar origin, the position of the origin of this muscle is not affected by movements of the radius in *Macrotus*. The tendons of this muscle are thick in *Eumops* and *Myotis* and the elasticity of the bellies is greatly reduced by connective tissue. Any proximal movement of the origin of this muscle is therefore transmitted to the pisiform through the relatively non-elastic muscle. Accordingly, probably with little muscular effort on the part of this muscle, the fifth digit is flexed when the radius is flexed, and the digit is allowed to extend to roughly a right angle to the humerus when the radius is extended. Because this muscle does not allow the fifth digit to extend

beyond this point, the distal part of the wing membrane is kept tautly spread when the wing is extended.

The transfer to the flexors and extensors of the radius—the biceps and triceps groups respectively—of much of the work of controlling the distal part of the wing serves the important end of keeping the sizes of the forearm muscles in bats to a minimum. This transfer is well illustrated by the M. flexor carpi ulnaris in *Eumops* and *Myotis*, and by the Mm. extensor carpi radialis longus and brevis in all three genera.

M. palmaris longus (median nerve)

ORIGIN.—From anterior base of spinous process of medial epicondyle.

INSERTION.—By aponeurosis, on anteroventral surface of carpus, on thumb pad, and on ventral surface of M. abductor digiti quinti.

REMARKS.—In *Eumops* this muscle has a tendinous origin, and the narrow belly extends along roughly the proximal half of the forearm. The slender distal tendon broadens into a thin aponeurosis that lies superficial to all the tendons on the ventral surface of the carpus. The aponeurosis divides into two parts at the base of the carpus; one passes craniad to the thumb, and the other passes caudad to the fifth digit. This latter part of the aponeurosis is much reduced in size in some specimens. I failed to find any trace of this muscle in *Myotis*. In *Macrotus* the fleshy origin is from the distal edge of the medial epicondyle and on the proximal part of the belly of the M. flexor digitorum profundus. The muscle is short and robust, and gives way to a strong tendon roughly one quarter of the way along the radius. The tendon divides into two parts at the carpus. The first tendon spirals around to the anterior surface of the thumb where it inserts on the anterior surface of the distal end of the first metacarpal; the second tendon passes to the ventral base of the third digit where it divides into two fascial sheets that insert on each side of the ventral surface of the proximal fifth of the third metacarpal.

ACTION.—In *Eumops* this muscle is a weak flexor of the first and fifth metacarpals. In *Macrotus* the muscle is relatively larger than in *Eumops*, and acts to flex and rotate the first metacarpal, and flex the third metacarpal. Perhaps the reduction of this muscle in *Eumops*, and its loss in *Myotis*, is correlated with the specialization of the M. extensor carpi ulnaris and the M. flexor carpi ulnaris as efficient flexors of the distal part of the wing in these bats.

M. flexor carpi radialis (median nerve)

ORIGIN.—From distal part of posterior border of M. pronator teres.

INSERTION.—Into fascia at ventral base of first metacarpal.

REMARKS.—In *Eumops* and *Myotis* this muscle is vestigial. In *Eumops* it arises by a thin, delicate tendon from the surface of the M. pronator teres and has no separate belly. In *Myotis* the muscle has a tiny belly 2 mm. long that lies on the distal surface of the M. pronator teres. The distal part of the tendon is extremely small, and could not be traced beyond the level of the base of the carpus. In *Macrotus* the muscle is robust, being roughly the same size as the M. palmaris longus, and takes fleshy origin from the central tendon and belly of the middle third of the M. pronator teres. The tendon of insertion is no smaller than the other flexor tendons of the forearm, and inserts on the ventral base of the third metacarpal.

ACTION.—In *Macrotus* this muscle flexes the third digit. In *Eumops* and *Myotis* the muscle is probably functionless; its extreme reduction in these genera may be correlated with the development of the M. extensor carpi ulnaris into a strong flexor of the third digit.

M. pronator teres (radial nerve)

ORIGIN.—By tendon, from anterior base of spinous process of medial epicondyle.

INSERTION.—Along roughly proximal eighth of medial surface of radius.

REMARKS.—In all three genera the muscle becomes broad and flat immediately distal to its origin, has a tendinous central part, and inserts fleshily on the shaft of the radius. In *Myotis* and *Macrotus* the muscle inserts along the proximal third of the ventral surface of the radius. In *Macrotus* the origin is on the proximal part of the medial epicondyle. The central tendon is larger than in the other genera, and from its middle third the M. flexor carpi radialis takes origin.

ACTION.—In bats, because of the nature of the elbow joint, pronation of the forearm can not occur. Therefore, this muscle is a weak flexor of the forearm. The most important function of this muscle in bats is that of steadying the elbow joint. The relatively small size of this muscle in *Eumops* may be due to the especially strong humeroradial articulation in this genus.

M. flexor digitorum profundus (median nerve)

ORIGIN.—From anteromedial surface of ulna and roughly proximal three fifths of posterior border of radius, by fleshy attachments.

INSERTION.—On ventral base of second phalanx of thumb and on ventral base of fifth digit.

REMARKS.—In *Eumops* this is the largest muscle of the flexor group of the forearm. The broad tendon passes immediately medial to the proximal end of the pisiform and deep to the scaphoid-pisiform ligament, dividing into two parts at this point. In *Myotis* the origin is from the spinous process of the medial epicondyle, from fascia on the medial epicondyle, and from the second fifth of the posterior border of the radius; the insertion is on the ventral surface of the second phalanx of the thumb, the ventral surface of the shaft of the second phalanx of the third digit, and the ventral tip of the third phalanx (cartilaginous) of the fourth digit. In *Macrotus* the muscle takes fibrous origin from the distal part of the medial epicondyle, and fleshy origin on the surface of the M. pronator teres and M. flexor carpi ulnaris; the insertion is on the ventral base of the second phalanx of the thumb, and on the ventral base of the third phalanx of the third digit.

ACTION.—In *Eumops* the muscle is a ventral flexor of the thumb and of the phalanges of the fifth digit. In *Myotis* the action is ventral flexion of the thumb and of the phalanges of digits three and four. The tendon to the thumb is the largest, and that to the fourth digit is the smallest of the three tendons of insertion. In *Macrotus* the muscle flexes the thumb and the phalanges of digit three. In *Myotis* and *Macrotus* this muscle can also cause posterior flexion of digits three and four and digit three respectively.

Flexion of the thumb while the bat is in flight lowers the distal end of the propatagium, thereby increasing the camber of the proximal part of the wing. By acting to flex the phalanges of any of the last three digits during the

downstroke this muscle resists the force of the air pressure that tends to produce dorsal flexion of both the metacarpal and phalangeal segments of the digit. In *Eumops* the tendon to the fifth digit helps maintain the optimal camber of the plagiopatagium during the downstroke by acting as a ventral flexor of the phalanges. Because of the great aerodynamic importance of this action, I can not understand why the tendon to the fifth digit is not retained in *Myotis* and *Macrotus*.

Extensor Group of Manus

M. interosseus dorsale

ORIGIN.—From posterodorsal base of second metacarpal.

INSERTION.—On anteroventral base of first phalanx of third digit.

REMARKS.—This muscle is present only in *Eumops*. The belly of the muscle lies opposite the proximal third of the third metacarpal. The large, flat tendon extends along the first half of the metacarpal on the anterodorsal surface, then spirals ventrad to a sesamoid bone that lies on the anteroventral surface of the third metacarpophalangeal joint. The sesamoid is attached by a short ligament to the anteroventral base of the first phalanx; the distal part of the tendon and the sesamoid bone are bound to the joint by a thick sheet of fascia.

ACTION.—Only in *Eumops* does flexion and extension of the first phalanges of the third and fourth digits occur in the anteroposterior plane. Therefore, this muscle extends the first phalanx of the third digit and partly spreads the distal part of the wing.

Flexor Group of Manus

I did not determine the innervations of the intrinsic muscles of the hand, and identified them on the basis of topographic relationships. Because these relationships in bats differ from those in other mammals, comparisons are difficult. In addition, the terminology of the muscles of the hand has not been uniformly applied and the homologies are not completely understood (Rinker, 1954:84). In connection with my work, I found it especially difficult to identify the muscles of the fifth digit. The names M. abductor digiti quinti and M. opponens digiti quinti are only tentatively applied; the two muscles may not be homologous with the muscles bearing the same names in other mammals.

M. abductor pollicis brevis

ORIGIN.—From posteroventral surface of trapezium and ligament between ventral base of second metacarpal and trapezium.

INSERTION.—Into the anteroventral part of pad on ventral surface of first metacarpophalangeal joint (thumb pad).

REMARKS.—The relationships of this muscle are approximately the same in all three genera. The muscle is short and robust in *Eumops*, being relatively largest in this genus. The muscle is thin, delicate and smallest in *Macrotus* and originates largely on the fascia on the ventral surface of the trapezium.

ACTION.—This muscle abducts and flexes the first digit.

M. flexor pollicis brevis

ORIGIN.—From anteroventral surface of base of second metacarpal, from adjacent ligament that extends from trapezium to second metacarpal, and from tendon of M. flexor digitorum profundus at level of first metacarpal.

INSERTION.—Into posteroventral part of thumb pad.

REMARKS.—This muscle is roughly the same in *Eumops* and *Myotis*, but is relatively larger in the former. In *Macrotus* the muscle is thin and delicate and has no part that takes origin from the tendon of the M. flexor digitorum profundus.

ACTION.—This muscle is a ventral flexor of the first metacarpal.

M. abductor pollicis

ORIGIN.—From along first 3 mm. of posteroventral surface of second metacarpal.

INSERTION.—By small tendon on dorsal base of second phalanx of thumb, and on lateral border of tendon of M. extensor pollicis brevis where this tendon passes over dorsum of first phalanx of thumb.

REMARKS.—In *Eumops* this muscle is short and robust. It is relatively smaller in *Myotis*; the origin is more restricted and the insertion is on the lateral surface of the first metacarpophalangeal joint and on the tendon of the M. extensor pollicis brevis where it crosses the joint. The muscle is absent in *Macrotus*.

ACTION.—In *Eumops* and *Myotis* this muscle adducts and rotates the thumb.

M. adductor digiti secundi

ORIGIN.—From first 9 mm. of ventral surface of second metacarpal, by fleshy attachment.

INSERTION.—By tendon, on posteroventral surface of trapezium.

REMARKS.—In *Myotis* this muscle is relatively smaller than in *Eumops*, but the attachments are similar. In *Macrotus* the muscle is absent.

ACTION.—This muscle acts as a posterior flexor of the second digit and thus serves to fold the distal part of the wing.

M. abductor digiti quinti

ORIGIN.—From posterior border of scaphoid.

INSERTION.—On ventral surface of fifth metacarpophalangeal joint.

REMARKS.—In *Eumops* this muscle takes origin by a broad, thick tendon, which extends distad over the entire belly of the muscle as a glistening fascial sheet. The tendon of insertion is also large and flat, and attaches to the strong fibrous sheath that covers the fifth metacarpophalangeal joint. In *Myotis* the origin is from the pointed tubercle that projects posteriorly from the proximal end of the pisiform; the tendon divides distally and inserts on either side of the fifth metacarpophalangeal joint. In *Macrotus* this muscle is represented by a strong tendon, which runs from the radial sesamoid to the fifth metacarpophalangeal joint. A fusiform bundle of fibers attaches onto the dorsal surface of the proximal part of the tendon. This bundle originates on the pisiform.

ACTION.—This muscle reinforces the fifth metacarpal against the force of the air pressure created during the downstroke, and braces the fifth carpometacarpal articulation. Because the muscle is also a weak flexor of the first phalanx of the fifth digit, it helps hold the proper camber in the distal part of the digit and resists the upward force of the air pressure against the wing membrane.

In the discussion of the action of the pectoralis group of muscles, the importance of the fifth digit in controlling the angle of attack of the plagiopatagium, and hence the amount of lift created by this part of the wing, was stressed. In *Eumops* the M. abductor digiti quinti is specialized to act as a powerful, partially elastic band that helps maintain the camber of the fifth metacarpal. The large tendons of the muscle, and the complete covering of the belly by thick fascia, strongly reduces the elasticity of the muscle. Thus, probably with little muscular effort, the muscle can act like a strong bowstring, and can resist forces that tend to straighten the dorsally bowed metacarpal. The effectiveness of this action is increased by contraction of the M. abductor pollicis longus, which pulls the scaphoid craniad and proximad. This pull increases the distance between the origin and insertion of the M. abductor digiti quinti. In addition, due to the structure of the carpus, extension of the fifth digit increases the distance between the scaphoid and the base of the fifth metacarpal, thus tending to stretch the muscle. In *Eumops* and *Macrotus,* because of its origin on the scaphoid, this muscle spans the ventral surface of the fifth carpometacarpal articulation and keeps the joint from allowing slight dorsal extension of the fifth metacarpal during the downstroke of the wings. In *Macrotus* the muscle is nearly non-elastic owing to the tendon that extends throughout the length of the muscle, and its action is probably similar to that in *Eumops.* In *Myotis,* however, the muscle is smaller and seemingly weaker than in the other genera. Perhaps powerful bracing of the fifth metacarpal is not needed in a small bat.

M. adductor digiti quinti

ORIGIN.—Along first 4 mm. of posteroventral surface of second metacarpal.

INSERTION.—Along proximal fifth of anteroventral surface of fifth metacarpal.

REMARKS.—This muscle is present only in *Eumops,* is broad and thin, and is one of the largest muscles of the manus.

ACTION.—This muscle is a flexor of the second digit. Because the M. flexor carpi ulnaris will not allow extension of the fifth digit beyond a right angle to the radius when the wing is fully extended, and flexes the fifth digit fully when the forearm is flexed, the M. adductor digiti quinti must act mainly to fold the distal part of the wing by flexing the second digit. This muscle is probably of importance mainly in folding the distal part of the wing when the bat is at rest, and in holding the wing in a fully flexed position during terrestrial locomotion. The retention of this muscle in *Eumops,* and its complete loss in the other two genera, is probably correlated with the importance of terrestrial locomotion in *Eumops.*

M. opponens digiti quinti

ORIGIN.—From distal end of pisiform.

INSERTION.—On ventral surface of fifth metacarpophalangeal joint immediately lateral to insertion of M. abductor digiti quinti.

REMARKS.—This muscle is similar in all three genera. It has a tendinous origin and insertion, and is smaller than the overlying M. abductor digiti quinti.

ACTION.—This muscle acts with the M. abductor digiti quinti to brace the fifth metacarpal, to flex partly the first phalanx of the fifth digit, and to steady the fifth carpometacarpal articulation.

Mm. interossei

There are four of these muscles on the ventral surface of the manus; their arrangement is as follows:

(1) ORIGIN.—From posteroventral base of second metacarpal and distal part of tendon of M. adductor digiti secundi. INSERTION.—On posterior surface of third metacarpophalangeal joint.

(2) ORIGIN.—From proximal end of pisiform. INSERTION.—On posterior surface of proximal end of first phalanx of third digit.

(3) ORIGIN.—Along posteroventral base of third metacarpal and anteroventral base of fourth metacarpal. INSERTION.—On anteroventral surface of fourth metacarpophalangeal joint.

(4) ORIGIN.—On sesamoid bone that lies on posteroventral base of fourth metacarpal. INSERTION.—On posteroventral surface of fourth metacarpophalangeal joint.

REMARKS.—In *Eumops* the anterior interosseus muscle of the fourth digit is especially large. The posterior interosseus muscle of the third metacarpal is small in this genus, and was not found in *Myotis* or *Macrotus*. In these two genera the interosseus muscles of the fourth metacarpal originate on the unciform.

ACTION.—These muscles function principally to brace the third and fourth metacarpals against the air pressure during the downstroke, but the muscles act also as weak flexors of the phalanges of the third and fourth digits. In *Eumops*, because the first phalanx of the fourth digit flexes posteriorly instead of ventrally as in the other two genera, the anterior interosseus muscle of this digit extends the first phalanx.

Muscles of Pelvic Girdle and Limb

M. psoas minor (lumbar nerves)

(This muscle should be listed separately as belonging to the myotomic musculature; it is placed here with the pelvic girdle musculature for the sake of convenience.)

ORIGIN.—From a strip roughly 1 mm. wide along ventrolateral surfaces of bodies of lumbar vertebrae two to four.

INSERTION.—On tip of pubic spine.

REMARKS.—In *Eumops* this muscle inserts by a large cylindrical tendon that extends craniad as a heavy fascial sheet to the ventral surface of the last lumbar vertebra. The middle of the belly of the muscle is dorsoventrally flattened. The muscle is fleshy for roughly two thirds of its length. In *Myotis* the origin is from the ventrolateral surfaces of the first three lumbar vertebrae; the insertion is on the pubic spine by a flat tendon that comprises half the length of the muscle. In *Macrotus* the origin is from the ventrolateral surfaces of the bodies of the last thoracic and first three lumbar vertebrae, and by a few muscle fibers on the M. psoas major. The muscle

is relatively largest in *Macrotus,* being thick and cylindrical in this genus. The fleshy part of the muscle extends almost to the insertion.

ACTION.—Contraction of this muscle tends to pull the ventral part of the pelvis forward, thereby arching the lumbar section of the vertebral column. This action may be useful in helping to double up the body when the bat is grooming itself or when an insect is being pinned against the uropatagium while the jaws adjust their grip on the prey. In all three genera this muscle is so robust and inserts by so heavy a tendon, however, that it seems it must perform some function, in addition to those mentioned above, that demands powerful action. This function may be to help brace the dorsally arched vertebral column while the bat is flying, and, at least in *Macrotus,* when the bat alights. During flight the bracing would be against the shock transmitted by the hind limbs and tail to the vertebral column when the air stream suddenly strikes the ventral surface of the uropatagium in rapid maneuvers. In *Macrotus* the shock of the bat's alighting is passed from the hind limbs through the pelvis to the vertebral column, and tends to straighten the dorsally arched column. By acting as a strong elastic brace, extending from the anteroventral part of the pelvis to the last thoracic vertebra, this muscle may absorb part of this shock. The large size of this muscle in *Macrotus* may be associated primarily with this bat's unique method of alighting.

Iliacus Group

M. iliacus (femoral nerve)

ORIGIN.—From lateral surfaces of bodies of lumbar vertebrae two to five, from lateral half of ventral surface of expanded anterior end of ilium, and from all but posterior 3 mm. of lateral edge of ilium.

INSERTION.—On low knob at distal end of lesser tuberosity of femur.

REMARKS.—In all three genera this muscle has a thick fibrous insertion. In *Myotis* the origin is from the lateral surfaces of the bodies of lumbar vertebrae three and four, the lateral edge of the iliac crest, and the lateral border of the ilium. In *Macrotus* the origin is from the triangular lateral surface of the iliac crest, and the insertion is along roughly 1 mm. of the middle of the medial ridge of the femur. The muscle is short and robust in *Macrotus* and has no vertebral origin. This muscle is most evident superficially in *Macrotus,* for in this genus the muscle is pulled upward and away from the surrounding muscles by the dorsally directed femur.

ACTION.—This muscle flexes and rotates the femur. It is most effective as a rotator in *Macrotus,* for the insertion is on the medial ridge of the femur, which is especially high in this genus. In all three genera the rotation this muscle effects is comparable to supination in terrestrial mammals, but because of the unusual posture of the pelvic limb of bats the muscle pulls the femur forward and swings the lower leg ventrad and craniad. Due to the dorsal flexion of the bodies of these bats the anterior end of the pelvis is tilted upward. As a result, this muscle not only flexes the femur but draws it dorsad. In *Eumops* and *Myotis* this muscle is important in crawling. Contraction of the muscle helps accomplish the forward component of the stride and tends to bring the lower leg to a right angle with the substrate. In *Macrotus* this muscle is probably of major importance in connection with

movements made while the bat is hanging from the ceiling of a cave or grotto. Often when roosting this bat shifts its foothold slightly in preparation for hanging by one foot, or to change from one foot to the other for hanging. During this shifting of position the body is generally pulled toward the ceiling by the flexion of the hind limbs. This flexion is also made preparatory to launching into flight. Occasionally *Macrotus* "walks" slowly along the ceiling of a cave by swinging the body and gaining a new foothold with one foot while hanging on with the other. During this type of progression the pelvic limbs are more or less flexed. Much of the power for these flexion movements is supplied by the Mm. iliacus and gluteus medius.

The M. iliacus is equally important in connection with aerial locomotion. In all three genera this muscle, together with other members of the iliacus group, helps attain anteroposterior stability of the hind limb during flight by acting against the antagonistic extensors of the femur. Rotational stability of the pelvic limbs may be gained in part by the opposing rotary actions of this muscle and M. gluteus medius acting against the extensors of the femur. In *Eumops* and *Myotis*, when sudden changes of direction are demanded while the animals are foraging, the uropatagium may be pulled downward to change its angle of attack and hence affect the lift it develops or to increase its effectiveness as a braking surface. The M. iliacus helps in the lowering of the posterior margin of the uropatagium by rotating the femur and swinging the shank downward and forward. Because of the different position of the hind limb in *Macrotus* this muscle is seemingly not involved in spreading or lowering the uropatagium.

M. psoas major (femoral nerve)

ORIGIN.—From ventrolateral surfaces of bodies of last four lumbar vertebrae (lumbars three to six), from medial half of ventral surface of iliac crest, and by a short slip from ventrolateral surface of pubis just posterior to pubic spine.

INSERTION.—On entire anterior surface of lesser trochanter of femur, by fleshy attachment.

REMARKS.—In *Eumops* the origin of the muscle is immediately deep to that of the anterior part of the M. iliacus. The area of origin of the M. psoas major is approximately 0.5 mm. wide at the level of lumbar vertebrae three, but broadens posteriorly to cover most of the lateral and ventrolateral surfaces of the bodies of lumbar vertebrae five and six. In *Myotis* the origin is from the last three lumbar vertebrae (lumbars three to five). In *Macrotus* the muscle takes origin from the lateral and ventral surfaces of the bodies of the last four lumbar vertebrae (lumbars three to six), the ventrolateral surface of the iliac crest, the anterior half of the lateral rim of the ilium, and by a short slip from the flat dorsal surface of the pubic spine. This slip, which occurs in *Eumops* and *Macrotus*, is assumed to be part of the M. psoas major. This is not a certain identification, however, for the innervation of the slip was not determined.

ACTION.—This muscle flexes and rotates the femur. When *Eumops* and *Myotis* crawl, the entire iliacus group of muscles probably works together to move the leg forward at the start of the stride. The net effect of their common contraction is to pull the femur forward and upward, and to rotate the femur

in such a way as to bring the shank to a right angle with the substrate. In *Macrotus* by flexing the femur, this muscle helps in many movements made while the bat is roosting. The iliacus group probably functions as a unit during flight to help steady the hind limb.

M. pectineus (femoral and obturator nerves)

ORIGIN.—From base and lateral surface of pubic spine.

INSERTION.—Along 9 mm. of anteroventral surface of femur, starting roughly 3 mm. distal to lesser trochanter.

REMARKS.—In *Myotis* the origin is from the pubic spine, and the insertion is along 2 mm. of the anteroventral surface of the femur starting immediately distal to the insertion of the iliacus. The origin is from the posterior two thirds of the pubic spine in *Macrotus,* and the insertion is on the anterior surface of the ventral ridge of the femur. This muscle is relatively largest in *Eumops,* and the insertion extends farther distad than in the other genera. The muscle can therefore act on the femur most powerfully in *Eumops.*

ACTION.—Adduction and flexion of the femur.

Gluteal Group

M. tensor fasciae latae (gluteal nerve)

ORIGIN.—From posterodorsal border of iliac crest and neural spine of first sacral vertebra.

INSERTION.—On anterior border of M. gluteus maximus and center of lateral surface of femur.

REMARKS.—In *Myotis* the muscle arises from the posterodorsal edge of the iliac crest and the neural spines of sacral vertebrae one to three. The insertion is along the distal part of the anterior edge of the M. gluteus maximus and on the proximal end of the lateral ridge of the femur. In *Macrotus* the M. tensor fasciae latae is continuous with the M. gluteus maximus. That part of the sheet of muscle which originates from the posterodorsal edge of the iliac crest and the middorsal fascia over the first sacral vertebra probably represents the M. tensor fasciae latae. The insertion is along the anterior edge of the M. gluteus maximus.

ACTION.—This muscle abducts and flexes the femur. The functional significance of these actions is discussed in the remarks on the M. gluteus maximus.

M. gluteus maximus (gluteal nerve)

ORIGIN.—From neural spines and middorsal fascia of last three sacral vertebrae (sacral vertebrae two to four) and neural spine of first caudal vertebra.

INSERTION.—Along approximately 3 mm. of middle of lateral surface of femur.

REMARKS.—Relative to the total mass of the muscles of the thigh, this muscle is larger in *Eumops* than in the other genera. In *Myotis* the origin is from the middorsal fascia and neural spines of the last two sacral vertebrae (sacral vertebrae three and four) and the neural spine of the first caudal vertebra. The insertion is along roughly the second fifth of the lateral surface of the femur, starting on the tubercle at the distal end of the lateral ridge of the femur. In *Macrotus* the origin is from the fused neural crests of the last

four sacral vertebrae (sacral vertebrae two to five) and the neural spine of the first caudal vertebra. The insertion is on the posterior surface of the M. rectus femoris and along roughly the middle third of the anterolateral surface of the femur.

ACTION.—This muscle, together with the M. tensor fasciae latae, abducts the femur and flexes it when the hind limb is extended. Seemingly, the primary function of these muscles is to help control the stability of the pelvic limbs during flight by acting against the antagonistic adductors of the femur.

The hind limbs serve as the base for the posterior part and trailing edge of the plagiopatagium. Dorsoventral movements of the hind limbs while the bat is in flight change the camber and angle of attack of the plagiopatagium, as well as lowering or raising the uropatagium. It is of great importance, therefore, that during flight the hind limbs be stabilized at the proper angle to maintain the aerodynamic efficiency of the flight membranes. There are a number of forces tending to move the hind limbs during flight. The force of the air stream against the uropatagium tends to move the limbs. Particularly at the top of the upstroke and bottom of the downstroke of the wings, the elastic wing membranes tend to disrupt the dorsoventral stability of the hind limbs. At all times while the wings are extended, the wing membranes pull laterally with considerable force on the pelvic limbs, and when the bat is in flight the air pressure against the wing membrane stretches them still further, increasing the lateral pull. Thus, while a bat is in flight, the hind limbs must partly resist forces tending to cause their adduction, abduction, and extension. The uropatagium is probably of some help in bracing the pelvic limbs against lateral pull, but the major burden of maintaining their rigidity is on the muscles of the pelvic girdle. For this reason, the functions of these muscles in bats can not be explained simply in terms of terrestrial locomotion, but rather should be considered in relation to both terrestrial and aerial locomotion. The latter has perhaps had the greater effect on the evolution of the hind limb musculature. Certainly, in bats that roost by hanging and that seldom practice any sort of terrestrial locomotion, the morphology of the pelvic limb must be in large part the result of adaptations for flight.

In *Eumops* and *Myotis,* then, the M. gluteus maximus acts to maintain the dorsoventral stability of the hind limb by resisting the downward pull caused by the wing membranes at the bottom of the downstroke. In *Macrotus,* due to the different position of the pelvic limbs, this muscle resists lateral pull on the limbs.

M. gluteus medius (gluteal nerve)

ORIGIN.—From posterodorsal edge of iliac crest and iliac fossa.

INSERTION.—On greater trochanter of femur.

REMARKS.—The origin extends onto the lateral surface of the neural spine of the first sacral vertebra in *Myotis.* In all three genera this is a thick, barrel-shaped muscle with a fleshy origin and insertion.

ACTION.—This muscle flexes, abducts and rotates the femur. In terrestrial locomotion this muscle helps in the forward part of the stride. Probably more important, however, is the action of bracing the hind limb during flight by acting with the iliacus group against the powerful, antagonistic extensors and adductors of the femur.

Quadriceps Femoris Group

M. quadriceps femoris (femoral nerve)

In the bats under study this muscle is composed of two parts, the M. rectus femoris and a muscle that probably represents, in *Eumops* at least, the fused Mm. vastus lateralis, vastus medialis and vastus intermedius. In the other two genera the part of the M. quadriceps femoris that originates on the femur is probably homologous with the M. vastus lateralis in other mammals. For the sake of convenience, the femoral division of the quadriceps is here called the M. vastus lateralis, although all of it may not be homologous with this muscle in other mammals.

ORIGIN.—M. rectus femoris: from lateral edge of ilium immediately anterior to acetabulum. M. vastus lateralis: from greater trochanter, from proximal two thirds of anterolateral surface and entire anterior surface of femur.

INSERTION.—On proximal end of patella.

REMARKS.—In *Eumops* the *M.* rectus femoris has a fibrous origin *via* a small sesamoid bone. The M. vastus lateralis attaches fleshily to the posterior surface of the M. rectus femoris throughout the length of the latter. The two muscles merge roughly half way along the femur and form a broad, flat tendon of insertion. In *Eumops* the M. vastus lateralis is approximately twice as large as the M. rectus femoris. In *Myotis* this muscle takes origin from a small tubercle immediately anterior to the acetabulum. The M. vastus lateralis originates on the anterior surface of the greater trochanter and the proximal third of the anterolateral surface of the femur. In *Macrotus* the M. rectus femoris has an unusually strong origin *via* a sesamoid bone on the anterodorsal rim of the acetabulum, and is larger than the M. vastus lateralis. This muscle originates from the greater trochanter and by fleshy attachment along the proximal fourth of the lateral surface of the femur. In *Macrotus* the tendons of insertion of these two muscles remain separate, but are bound in a common fascial sheath.

ACTION.—This muscle extends the shank at the end of the rearward component of the stride in *Eumops* and *Myotis* but probably is even more important in steadying the shank during flight. The muscles that flex the shank and supply most of the resistance to the lateral pull exerted by the wing membranes are the gracilis, the semimembranosus and the semitendinosus. These are among the largest muscles in the pelvic girdle, and they are directly antagonistic to the M. quadriceps femoris. This muscle must act against these flexors throughout most of the time that the bat is in flight. The lateral pull caused by the wing membranes is greatest during the downstroke of the wing, but is greatly reduced in the upstroke largely because the wings are then partly folded. This intermittent pull is probably not resisted by intermittent contractions of the flexors of the shank, for this would demand considerable energy at a time when a premium is placed on energy conservation. It is likely that simply the tonus or weak contractions of the powerful flexors of the shank and the M. quadriceps femoris is sufficient to steady the shank during level flight. Powerful bracing action, calling for strong contractions of many of the muscles of the pelvic girdle, may be needed only while the bat is making rapid maneuvers to catch insects or avoid obstacles. In the course of these maneuvers the wings often beat more rapidly than usual and are moved into positions

causing more air pressure to be directed against the membranes of the wing.

The retention of a large, powerful M. quadriceps femoris in *Macrotus*, a bat that seldom uses terrestrial locomotion, suggests that this muscle has an important function connected with flight. Because of the 180 degree rotation of the hind leg in *Macrotus*, contraction of this muscle has a different function in relation to flight in this genus from that in the other genera, although the action (extension of shank) is the same. In *Macrotus* this muscle helps control the dorsoventral stability of the shank and resists the downward pull of the plagiopatagium at the bottom of the downstroke of the wings. In addition, the placement of the origin of the M. rectus femoris and the length of its belly and tendon help direct the femur dorsad. Aerodynamically, this function is important. The entire vertebral column of *Macrotus* is arched sharply dorsad with the result that the long axis of the pelvis is nearly dorsoventral. Therefore, to create the proper angle of attack and camber of the plagiopatagium, the hind legs must be held in a spider-leg-like posture with the femur directed dorsad. The large size of the M. rectus femoris and the shift of its origin toward the dorsal rim of the acetabulum in *Macrotus* is probably associated with the peculiar posture of the pelvic limb in this genus.

Tibial Extensor Group

M. extensor digitorum longus (deep peroneal nerve)

ORIGIN.—From lateral condyle of femur and posterior border of M. extensor hallucis longus.

INSERTION.—On dorsal bases of distal phalanges of digits two to five.

REMARKS.—In all three genera the tendon is undivided as far distally as the dorsum of the tarsus; there the tendon divides into the tendons that continue to the insertions on the digits. In *Eumops* the fleshy part of this muscle lies along the entire length of the shank. The muscle originates by a short tendon on the lateral condyle of the femur in *Myotis* and the belly extends along roughly the proximal two thirds of the shank. The insertion is on the dorsal bases of the distal phalanges of digits one to five. In *Macrotus* the origin is from the lateral condyle of the femur and along the lateral border of the proximal third of the tibia; the insertion is on digits one to five, as in *Myotis*. In *Macrotus* the belly of the muscle is relatively thinner than in the other genera, and lies approximately opposite the proximal half of the shank.

ACTION.—Extension of the digits of the foot.

M. extensor hallucis longus (deep peroneal nerve)

ORIGIN.—From lateral condyle of femur and anterior border of M. extensor digitorum longus.

INSERTION.—On medial surface of base of first metatarsal.

REMARKS.—This muscle is relatively much larger in *Eumops* than in the other two genera. In *Eumops* it is the anteriormost muscle of the shank, and is fleshy to the level of the distal part of the tarsus. In *Myotis* the origin is from all but the proximalmost 3 mm. of the posterior surface of the tibia, and from the lateral surface of the distal third of the fibula. The insertional tendon passes along the medial surface of the tarsus, is bound by fascia to the medial surface of the base of the first metatarsal, and inserts on the lateral surface of the base of the first phalanx of the first digit. This is an extremely delicate

muscle having a thin insertional tendon in *Macrotus*. The origin is by a narrow band of muscle fibers from the lateral surface of the distal half of the tibia; the insertion is on the medial base of the first metatarsal.

ACTION.—This muscle swings the foot craniad and dorsad. The large size of this muscle in *Eumops* is probably associated with this animal's roosting habits and well-developed ability to crawl. In the forward component of the stride the foot swings forward in order to increase the length and effectiveness of the stride; this movement is controlled largely by this muscle. Its degenerate nature in *Macrotus* is probably correlated with this bat's habit of roosting by hanging and the unimportance of terrestrial locomotion in this genus.

Mm. extensores breves (deep peroneal nerve)

ORIGIN.—There are seven of these muscles. The medial slip takes origin from the anterodorsal surface of the distal end of the fibula, and the lateral slip from the dorsal surface of the proximal part of the calcaneus. The other five slips originate on the tuberosity which projects dorsad from the distal part of the calcaneus.

INSERTION.—The medial slip inserts on the dorsomedial surface of the base of the first phalanx of the first digit, and the lateral slip on the dorsolateral surface of the base of the first phalanx of the fifth digit. The other five slips insert on the distal phalanges of digits one to five.

REMARKS.—There are no important differences in these muscles among the three genera.

ACTION.—Extension of the digits.

Peroneal Group

M. peroneus longus (peroneal nerve)

ORIGIN.—From posterior part of lateral condyle of tibia and proximal third of anterolateral surface of fibula.

INSERTION.—On ventrolateral base of fourth metatarsal.

REMARKS.—In *Eumops* the insertional tendon crosses to the lateral edge of the tarsus, passes over the dorsal surface of the cuboid, and through the space between the distal end of the calcaneus and the proximal end of the fifth metatarsel to the ventral surface of the foot. The belly of the muscle is broad and flat, and extends along roughly the proximal three quarters of the shank. The origin in *Myotis* is from the head and lateral surface of the proximal two thirds of the fibula. The insertional tendon follows approximately the same course as that in *Eumops*, but inserts on the ventral base of the third metatarsal. In *Macrotus* the origin is from the anterior surface of the base and the thin distal remnant of the fibula. The insertional tendon follows a course similar to that in the other two genera, but continues across the ventral bases of metatarsals three and four to which it is bound by fascia, and inserts on the base of the second metatarsal. In *Macrotus* the tendon of this muscle is the largest of the extensor tendons of the shank.

ACTION.—This muscle rotates the foot, tending to pull the lateral part of the foot dorsad and laterad. In terrestrial locomotion in *Eumops* and *Myotis* the result of the common contraction of this muscle and the M. gastrocnemius

is to pull the foot laterad and bring it into line with the shank, thus giving a final push at the end of the propulsion stroke of the stride. In *Macrotus* the rotation of the foot controlled by this muscle may be important in alighting, for in this maneuver the feet seem to be so rotated that the plantar surfaces tend to face one another. This muscle also helps to flex the foot and releases its grip on the substrate as *Macrotus* launches into flight.

M. peroneus brevis (peroneal nerve)

ORIGIN.—From approximately the middle half of anterolateral surface of fibula.

INSERTION.—On dorsolateral surface of base of fifth digit.

REMARKS.—The insertion in *Myotis* is on the dorsal surface of the shaft of the fifth metatarsal. The origin in *Macrotus* is from the anterolateral surface of the shaft of the fibula.

ACTION.—Flexion and rotation of the foot. In general, this muscle has the same action as the M. peroneus longus.

Adductor Group

M. gracilis (obturator nerve)

ORIGIN.—From posterior 3 mm. of insertional tendon of M. psoas minor and ventrolateral edge of pelvis from tip of pubic spine to posteroventral angle of ischium.

INSERTION.—By a common tendon with M. semitendinosus on posteromedial surface of tibia roughly one third of the way along shank.

REMARKS.—In *Eumops* this muscle and the M. semimembranosus are almost exactly the same weight and are the two largest muscles in the pelvic girdle. Among the bats under study, the M. gracilis is relatively largest in *Eumops*. In this genus the broad, flat belly extends nearly the length of the thigh and gives rise to a heavy tendon shared by the M. semitendinosus. In *Myotis* the origin is along approximately the anterior two thirds of the ventrolateral edge of the pelvis including the pelvic spine; the insertion is on the posterior surface of the tibia one sixth of the way along its length. The belly of the muscle in *Myotis* lies along the proximal half of the femur. In *Macrotus* the muscle arises from along the entire ventrolateral rim of the pelvis, including the pubic spine; the insertion is by a separate tendon on the posteromedial surface of the tibia one tenth of the way along the shank. The flat belly extends less than half way along the femur. The tendons of the M. gracilis and the Mm. semimembranosus and semitendinosus are separate and are not fused, but they are bound together by fascia and appear superficially to be a single tendon.

ACTION.—This muscle is a flexor of the shank and adductor of the hind limb. In *Eumops* and *Myotis* it is important in connection with both terrestrial and aerial locomotion. In *Macrotus* the M. gracilis is important in flight and by flexing the shank it aids in many movements made while the bat is roosting.

In *Eumops* and *Myotis* the M. gracilis helps support the weight of the body during terrestrial locomotion, but its importance as an adductor may be limited by its great power as a flexor of the shank. Only when flexion of

the shank is resisted by the antagonistic Mm. rectus femoris and vastus lateralis or by the grip of the claws on the substrate may the M. gracilis act as an adductor.

The large size of the M. gracilis in *Eumops* and *Myotis* and the fusion of the insertional tendon with that of the heavy M. semitendinosus seem to be associated more with the importance of the M. gracilis during flight than with its function in terrestrial locomotion. The fusion of the tendons of the Mm. gracilis and semitendinosus indicates that these muscles perform their most important function by working together. The action caused by their simultaneous contraction is flexion of the shank. This action, in which these muscles must usually be aided by the M. semimembranosus, helps steady the hind limb by bracing the shank against the lateral pull exerted by the wing membranes. Photographs of bats in flight show that the flexors of the shank are under tension during the downstroke of the wing, and it is probably at this time that the lateral pull by the wing membranes is strongest. In *Macrotus*, with its delicate flight membranes and slow flight, the lateral pull is probably not great. In *Eumops*, in contrast, the flight membranes are thick and leathery and strongly braced with elastic cartilage, and the flight is rapid. Accordingly, the lateral pull on the shank must be strong during the downstroke. In *Eumops* the pronounced specializations of the M. gracilis (the extension of its origin onto the insertional tendon of the M. psoas minor, the broad belly extending nearly the length of the shank, the complete fusion of its insertional tendon with that of the M. semitendinosus, and the distal position of the insertion) all serve the end of developing a strong system of flexors of the shank. These modifications have probably attended the development of speedy flight in this genus and are not primarily associated with its strong terrestrial locomotion.

In *Macrotus*, because of the posture of the pelvic limbs, the M. gracilis does not brace the shank against lateral pull but serves mainly to resist the dorsal pull by the wing membranes on the shank at the top of the upstroke and beginning of the downstroke. In general, this muscle acts against the Mm. rectus femoris and vastus lateralis to maintain the dorsoventral stability of the hind limb.

M. adductor longus (obturator nerve)

ORIGIN.—From lateral surface of ventral half of ascending ramus and posteroventral angle of ischium and from lateral surface of pubis posterior to pubic spine.

INSERTION.—Along roughly proximal third of posteromedial surface of femur starting immediately distal to lesser trochanter.

REMARKS.—In *Eumops* this is a large, robust muscle having fleshy attachments. The anterior part of the origin covers the entire lateral surface of the pubis from its ventral border to the ventral rim of the obturator fenestra. In *Myotis* the origin is from the lateral surface of the posteroventral angle of the ischium and the insertion is along the middle third of the posteromedial surface of the femur. In *Macrotus* the origin is along the lateral surface of the ventral border of the pelvis from the posteroventral angle of the ischium

to the base of the pubic spine; the insertion is on the proximal half of the medial ridge of the femur.

ACTION.—This muscle adducts the femur. The muscle is large in *Eumops* and *Myotis* and its insertion extends well beyond the lesser trochanter of the femur, thus enabling it to act powerfully on the femur. The muscle is relatively small in *Macrotus* and the insertion is situated farther proximad than in the other two genera. These differences are probably due to the contrasts between the functions of this muscle in the bats under discussion. This muscle supports the weight of the posterior part of the body during terrestrial locomotion in *Eumops* and *Myotis*, but in *Macrotus* it is used primarily for flight. Also, with the other adductors of the femur, this muscle aids in the dorsoventral stabilization of the pelvic limbs during flight in *Eumops* and *Myotis*. In *Macrotus*, because of the different position of the hind limbs, this function is largely taken over by other muscles. The femoral adductors in this genus seem to be more important in connection with erratic flight, in which the hind legs may be adducted—pulled downward to roughly their usual position in the other two genera—in order to increase the area of the uropatagium. Photographs of *Macrotus* hovering or turning sharply, show the legs adducted and the uropatagium spread. This movement is probably mostly under the control of the adductors of the femur.

M. adductor brevis (obturator nerve)

ORIGIN.—From along 3.5 mm. of lateral surface of ilium adjacent to posteroventral rim of obturator fenestra.

INSERTION.—Along 4 mm. of proximal part of posterolateral surface of femur starting on ridge of greater trochanter.

REMARKS.—In *Myotis* the muscle arises from the lateral surface of the ascending ramus of the ischium adjacent to the posterodorsal rim of the obturator fenestra; the insertion is along 1.5 mm. of the posteromedial surface of the femur starting just distal to the trochanteric fossa. In *Macrotus* the muscle originates on the lateral surface of the posteroventral angle of the ischium and inserts along the distal half of the medial ridge of the femur.

ACTION.—In *Eumops* this muscle adducts and rotates the femur; as a result the shank is pulled downward and tends to become vertical to the substrate. This muscle acts solely as an extensor of the femur in *Myotis*. In *Macrotus* the action adducts the femur.

This muscle (and most other muscles) probably does not act alone, but usually in co-operation with certain other adductors of the femur (adductor longus, pectineus and obturator externus) to steady the pelvic limb against the opposing abductors during flight. The net effect of the common action of the abovementioned adductors is not only adduction but also rotation of the femur; this rotator is counter to the rotation caused by the action of the main abductors (M. tensor fasciae latae, M. gluteus maximus and M. gluteus medius). During flight the antagonistic pull fo these two groups of muscles probably stabilizes the pelvic limbs.

In *Eumops* and *Myotis* this muscle functions in connection with terrestrial locomotion; in *Eumops* the action is to help support the posterior part of

the body and hold the shank vertical to the substrate, and in *Myotis* the muscle aids in the propulsion stroke of the hind limb.

M. adductor magnus (obturator nerve)

ORIGIN.—Along 4 mm. of dorsal border of obturator fenestra adjacent to ischial tuberosity.

INSERTION.—On posterior surface of greater trochanter of femur.

REMARKS.—The origin of this muscle is approximately the same in all three genera. In *Myotis* and *Macrotus* the insertion is along roughly 1 mm. of the posteromedial surface of the femur immediately distal to the level of the trochanters.

ACTION.—This muscle extends and rotates the femur. In *Eumops* the rotation tends to swing the shank downward and forward and orient it vertically to the substrate. In *Myotis* and *Macrotus* the rotation is in the opposite direction, and tends to pull the shank upward and backward.

M. obturator externus (obturator nerve)

ORIGIN.—Along 3 mm. of rim of obturator fenestra adjacent to posteroventral angle of ischium.

INSERTION.—On posteromedial surface of greater trochanter.

REMARKS.—In *Eumops* the insertion is by a short, flat tendon. In *Myotis* the origin is along the ventral half of the rim of the obturator fenestra; the fleshy insertion is in the trochanteric fossa. The attachments are similar in *Myotis* and *Macrotus*.

ACTION.—Extension and adduction of the femur.

Ischiotrochanteric Group

M. gemellus (sciatic nerve)

ORIGIN.—Along dorsal border of superior ramus of ischium from adjacent to posterior rim of acetabulum to superior tuberosity.

INSERTION.—On posterior surface of greater trochanter of femur.

REMARKS.—This muscle was not found in *Myotis*. In *Macrotus* it is a thin band of fibers extending from along 1 mm. of the dorsal rim of the superior ramus of the ischium immediately posterior to the acetabulum to the posterior cartilaginous rim of the acetabulum. This muscle seems to be a vestige of one or both of the gemellus muscles.

ACTION.—In *Eumops* this muscle is a weak extensor and rotator of the femur. In *Macrotus* the muscle is probably functionless.

Hamstring Group

M. caudofemoralis (tibial nerve)

ORIGIN.—From transverse process of last sacral vertebra and lateral surface of body of first caudal vertebra.

INSERTION.—Along proximal half of posterior surface of femur.

REMARKS.—In all three genera the insertion starts immediately distal to the level of the trochanters of the femur. In *Eumops* the posterior part of the origin is fibrous; otherwise the attachments are fleshy. In *Myotis* the origin is from the transverse process of the last sacral vertebra; the insertion is

along the proximal third of the posterior surface of the femur. The muscle takes origin in *Macrotus* from the posterior part of the transverse process of the last sacral vertebra and the transverse ridge of the first caudal vertebra. The insertion is along the proximal quarter of the posterolateral surface of the femur.

ACTION.—This muscle acts mainly to extend the femur. By acting against the flexors of the femur the muscle helps steady the hind limbs during flight. In terrestrial locomotion the muscle acts with the other members of the hamstring group of muscles to produce the rearward component of the stride. In *Macrotus,* in contrast to the other genera, the origin is on the posterolateral surface of the femur, and the muscle abducts as well as extends the femur. The action steadies the pelvic limb against the lateral pull of the wing membranes.

M. semitendinosus (tibial nerve)

ORIGIN.—From tip and lateral surface of rim of dorsal ischial tuberosity.

INSERTION.—On posterior surface of tibia one third of way along shank.

REMARKS.—This muscle and the M. gracilis insert by a common tendon in *Eumops* and *Myotis.* In the latter genus the origin of the M. semitendinosus is from the entire lateral surface of the dorsal ischial tuberosity; the insertion is on the posterior surface of the tibia one sixth of the way along the shank. In *Macrotus* this muscle takes origin by two heads: (1) from the entire lateral surface of the dorsal ischial tuberosity, by fleshy attachment; (2) from the middle of the dorsal border of the ischium, by fibrous attachment. The insertion is on the posterior surface of the tibia one eighth of the way along its length. The insertional tendons of the two heads are separate but are bound in a common fascial sheath. In *Eumops* and *Myotis* the M. semimembranosus is much larger than the M. semitendinosus. In *Macrotus* this situation is reversed; the first head of the M. semitendinosus is at least twice as large as either the second head or the M. semimembranosus.

ACTION.—This muscle extends the femur and flexes the shank. The functional significance of this action during flight in *Eumops* and *Myotis* is discussed in the account of the M. gracilis. In these genera the M. semitendinosus also provides much of the power for the propulsion part of the stride of the hind limb. In *Macrotus* this muscle helps steady the hind limb against the dorsal pull of the wing membranes by acting as a ventral flexor of the shank. The dorsal ischial tuberosity is turned more sharply mediad in *Macrotus* than in the other genera, thus putting the origin of the semitendinosus medial to the head of the femur. Because its origin is posterior and medial to the head of the femur this muscle is an effective abductor of the hind limb in the genus, and helps the Mm. gluteus maximus and caudofemoralis resist the lateral pull of the wing membranes. The flexor action of the M. semitendinosus is also important when *Macrotus* is making shifts in roosting posture and slight changes in roosting location.

M. semimembranosus (tibial nerve)

ORIGIN.—From lateral surface of superior tuberosity and caudal border of ischium.

INSERTION.—On posteromedial surface of tibia roughly one quarter of way along shank.

REMARKS.—In *Eumops* this muscle and the M. gracilis are the two largest muscles of the pelvic girdle. The M. semimembranosus inserts by a broad, flat tendon that comprises approximately two fifths of the length of the muscle. In *Myotis* the origin is on the lateral surface of the caudal border of the ischium. The insertion is on the posteromedial surface of the tibia roughly one sixth of the way along the shank, and the insertional tendon comprises half the length of the muscle. This muscle is relatively smaller in *Macrotus* than in the other genera. The origin in *Macrotus* is from the dorsal half of the caudal border of the ischium; the insertion is on the posterior surface of the tibia roughly one eighth of the way along the shank. The insertion of this muscle is proximal to that of the M. gracilis in all three genera, the separation of the tendons being greatest in *Eumops* and least in *Macrotus*.

ACTION.—This muscle extends the femur and flexes the shank. In *Eumops* and *Myotis* this muscle acts with the Mm. semitendinosus and caudofemoralis to supply most of the power for the propulsion part of the stride of the hind limb in quadrupedal locomotion. The origin of the M. semimembranosus is ventral to the acetabulum due to the tilting upward of the anterior end of the pelvis in these bats. Extension of the femur, therefore, results in pulling the femur caudad and ventrad, this action tending not only to help in the main propulsion movement of the stride of the hind limb but also to assist the adductors of the femur in supporting the weight of the posterior part of the body. This muscle is also a strong flexor of the shank, but when the bat is walking the hold the claws maintain on the substrate probably limits the flexor action of the muscles and causes it to function as an extensor of the femur. In *Macrotus*, by flexing the hind limb, this muscle would help in movements made while the bat is roosting.

This muscle is important during flight. In *Eumops* and *Myotis* it steadies the hind limbs against the lateral pull of the wing membranes, and in *Macrotus*, serves mainly to resist the dorsal pull exerted by the wing membranes.

M. biceps femoris (tibial nerve)

ORIGIN.—From lateral surface of tip of dorsal ischial tuberosity.

INSERTION.—On lateral condyle of tibia.

REMARKS.—In *Eumops* this is a thin, straplike muscle, and has a tendinous origin and insertion. In *Myotis* the muscle is absent. In *Macrotus* it is vestigial, being represented by a delicate strand of muscle approximately 0.25 mm. in breadth. The origin is from the fascia overlying the dorsal ischial tuberosity and the insertion is on the lateral surface of the knee.

ACTION.—This muscle flexes the shank and extends the femur in *Eumops*. In *Macrotus* the muscle is probably functionless due to its small size.

Flexor Group of Leg

M. gastrocnemius (tibial nerve)

ORIGIN.—Medial head: from posteroventral surface of femur immediately proximal to medial condyle. Lateral head: from posterior surface of head of fibula and lateral condyle of femur.

INSERTION.—On proximal end of calcaneus.

REMARKS.—The connections of this muscle are similar in all three genera. In *Eumops* the belly is robust and extends the length of the shank. The muscle is relatively more slender in *Myotis* and the belly gives way to the insertional tendon near the middle of the shank. In *Macrotus* the muscle is extremely slender; and roughly three quarters of its length is tendinous.

ACTION.—Extension of the foot.

M. plantaris (tibial nerve)

ORIGIN.—Along posterior surface of proximal two thirds of tibia and anteromedial surface of proximal half of fibula.

INSERTION.—On ventral surfaces of distal phalanges of digits one to five.

REMARKS.—In *Eumops* the large tendon of this muscle broadens into an aponeurosis in the plantar region and there is joined by the tendon of the M. flexor digitorum fibularis (Fig. 17). From this junction a tendon extends onto each digit. In *Myotis* the origin is from the posterior surface of the proximal two thirds of the tibia. The aponeuroses of the Mm. plantaris and flexor digitorum fibularis are fused at their distal ends in this genus, thus, they are not so completely fused as in *Eumops*. The origin of the M. plantaris in *Macrotus* is along the proximal half of the posterolateral surface of the tibia, from the tendon of the M. popliteus, and by a few fibers from the vestigial fibula. The tendon of the M. plantaris, which extends to the hallux, separates from the main tendon at the level of the proximal part of the tarsus and does not connect with the plantar aponeurosis. The degree of fusion of the two aponeuroses is similar in *Macrotus* and *Myotis*.

The unspecialized condition in mammals is for the plantaris tendon to divide into a superficial and a deep aponeurosis in the plantar region; the ventral surface of the deep part serves as origin for the M. flexor digitorum brevis. Deep to the two plantar aponeuroses and separate from them, lies the aponeurosis of the M. flexor digitorum fibularis, from which arise the Mm. lumbricales. The bat genera considered here differ from this general plan in the following ways: the superficial plantar aponeurosis is absent; the M. flexor digitorum brevis is completely separate from the tendon of the M. plantaris; the deep plantar aponeurosis is fused distally to that of the M. flexor digitorum fibularis; the Mm. lumbricales originate on the ventral surface of the plantar aponeurosis. Seemingly, in the evolution of bats, the M. flexor digitorum brevis gained an origin separate from the deep plantar aponeurosis, and the deep plantar aponeurosis fused with the aponeurosis of the M. flexor digitorum fibularis and shared its insertional tendons. Probably due to the fusion of these two aponeuroses the Mm. lumbricales have been crowded from the aponeurosis of the M. flexor digitorum fibularis onto the ventral surface of the deep plantar aponeurosis.

ACTION.—Flexion of the digits of the foot. The fusion of the tendons of the M. plantaris and the M. flexor digitorum fibularis indicates that these muscles normally work together. Judging by the size of these muscles and their tendons, together they form the strongest functional unit in the shank. The muscles enable the bat's claws to grip the substrate.

M. popliteus (tibial nerve)

ORIGIN.—On medial surface of head of fibula.

INSERTION.—Along proximal half of posterolateral surface of tibia.

REMARKS.—In *Eumops* the muscle is thick and fleshy proximally, becoming thin and fibrous distally. It is represented in *Myotis* by a thin strand of muscle extending from the posterior surface of the lateral condyle of the tibia to the posterior surface of the tibia immediately distal to the head. In *Macrotus* the origin is from the posterior and medial surfaces of the vestigial head of the fibula; the insertion is along the proximal eighth of the posterior surface of the tibia. The muscle is short and thick in this genus and fills most of the concavity in the posterior surface of the tibia immediately distal to the head.

ACTION.—This muscle binds together the heads of the tibia and fibula and braces the proximal parts of these bones. The muscle is vestigial and functionless in *Myotis*. In *Macrotus* the muscle pulls the small head of the fibula caudad and mediad and helps brace the knee joint.

M. tibialis posterior (tibial nerve)

ORIGIN.—From along distal two thirds of medial surface of fibula, and from medial surface of interosseus membrane and anterior surface of M. flexor digitorum fibularis.

INSERTION.—On ventral surface of tarsus.

REMARKS.—In *Eumops* the tendon of this muscle spreads out on the ventral surface of the navicular, is bound to it by fascia, and sends flat tendinous bands to the distal part of the ventral surface of the calcaneus, and the ventral surfaces of the cuboid and internal cuneiform. In *Myotis* the muscle lies opposite the distal third of the shank, and takes origin from the posterior surface of the tibia, the anteromedial surface of the M. flexor digitorum fibularis, and the medial surface of the M. peroneus longus; the insertion closely resembles that in *Eumops*. The muscle originates in *Macrotus* along the distal three quarters of the posterolateral surface of the tibia and the adjacent medial surface of the M. flexor digitorum fibularis. The insertion is on the ventral surface of the navicular.

ACTION.—Extension of the foot.

M. flexor digitorum fibularis (tibial nerve)

ORIGIN.—Along all but distalmost 3 mm. of posteromedial surface of fibula.

INSERTION.—On ventral surfaces of distal phalanges of digits one to five.

REMARKS.—The differences between the insertions of this muscle in the three genera of bats under study are described in the account of the M. plantaris. The origin in *Myotis* is on the lateral condyle of the tibia and along the entire posterior surface of the fibula. In *Macrotus* the muscle originates on the lateral surface of the vestigial head of the fibula and on the posterior surface of the shaft of the fibula.

ACTION.—Flexion of the digits of the foot.

Flexor Group of Pes

M. flexor digitorum brevis (tibial nerve)

ORIGIN.—From dorsal surface of proximal end of calcaneus.

INSERTION.—On lateral surfaces of second phalanges of digits two to four.

REMARKS.—The tendon of each slip divides at the level of the proximal end of the first phalanx and sends a tendon on either side of the insertional

tendon used by the M. plantaris and the M. flexor digitorum fibularis. In all three genera the latter is a thin muscle having slender and delicate tendons. In *Macrotus* there is an extra slip from which a tendon extends to the fifth digit. The unusual topographic relationships of this muscle are discussed under the M. plantaris.

ACTION.—Flexion of digits two to four in *Eumops* and *Myotis* and digits two to five in *Macrotus*.

M. abductor hallucis brevis (tibial nerve)

ORIGIN.—From distal edge of medial tarsal bone.

INSERTION.—On medial sesamoid bone of first metatarsophalangeal joint.

REMARKS.—The medial tarsal bone is much larger and this muscle has a more extensive origin in *Eumops* than in the other genera. Otherwise this entirely fleshy muscle has similar attachments in all three genera.

ACTION.—Abduction of the hallux. This muscle and the M. abductor digiti quinti spread out the foot by abducting the medial and lateral digits. Photographs of *Eumops* running show that the medial and lateral digits are abducted while the foot is on the ground; this probably gives the foot a firmer purchase on the substrate.

M. abductor ossis metatarsi quinti (tibial nerve)

ORIGIN.—From middle of ventrolateral surface of calcaneus.

INSERTION.—On lateral edge of plantar aponeurosis.

REMARKS.—This muscle usually lies deep in the tendon of the M. plantaris and inserts on the fifth metatarsal. In the bats considered here, however, the muscle passes mediad, ventral to the tendon of the M. flexor digitorum fibularis, to insert on the side of the plantar aponeurosis. My identification of this muscle is tentative.

ACTION.—This muscle pulls the plantar aponeurosis laterad and proximad. In all three genera when the foot is relaxed it is not in line with the plane of movement of the shank, but is turned inward. The tendons of the Mm. plantaris and flexor digitorum fibularis must, therefore, turn mediad at the level of the base of the tarsus. In *Eumops*, in which the inturning of the foot is most pronounced, the angle of the turn is approximately 45 degrees. When these muscles contract, the tendons tend to straighten, pulling the foot back toward an alignment with the plane of action of the shank and forcing the tendons toward the medial edge of the tarsus. Contraction of the M. abductor ossis metatarsi quinti reduces the latter force by pulling the tendons of the Mm. plantaris and flexor digitorum fibularis toward the lateral side of the foot, thus effecting some straightening of these tendons. In addition, by pulling the plantar aponeurosis proximad this muscle helps flex the digits.

M. abductor digiti quinti (tibial nerve)

ORIGIN.—From ventral surface of distal part of calcaneus and from ventral surface of lateral half of expanded base of fifth metatarsal.

INSERTION.—On lateral sesamoid bone of fifth metatarsophalangeal joint.

REMARKS.—This muscle has fleshy attachments and similar topographic relationships in all three genera.

ACTION.—Abduction of the fifth digit.

M. adductor hallucis (tibial nerve)

ORIGIN.—From ventral surfaces of bases of second and third metatarsals and raphe between this muscle and M. adductor digiti quinti.

INSERTION.—On lateral surface of base of first phalanx of first digit and lateral sesamoid bone of first metatarsophalangeal joint.

REMARKS.—This muscle shows only minor variation between the three genera studied.

ACTION.—Adduction of the hallux.

M. adductor digiti quinti (tibial nerve)

ORIGIN.—From ventral surfaces of bases of metatarsals two and three and from raphe between this muscle and M. adductor hallucis.

INSERTION.—On medial surface of base of first phalanx of fifth digit and medial sesamoid of fifth metatarsophalangeal joint.

REMARKS.—This muscle is essentially the same in all three genera.

ACTION.—Adduction of the fifth digit.

Mm. lumbricales (tibial nerve)

ORIGIN.—From the ventral surface of the plantar aponeurosis.

INSERTION.—On dorsal surfaces of second phalanges of digits one to five.

REMARKS.—There are nine of these muscles. They send a tendon spiraling dorsad around each side of the bases of the first phalanges of digits two to five, and around the medial surface of the first digit. In *Myotis* these muscles originate between the bases of the insertional tendons that extend distad from the plantar aponeurosis. These muscles are relatively more slender in *Macrotus* than in the other genera, and have similar attachments to those in *Eumops*.

ACTION.—Flexion of the digits of the foot.

Mm. interossei (tibial nerve)

ORIGIN.—By ten slips, two on each digit, one from lateral and one from medial surface of bases of metatarsals one to five.

INSERTION.—On lateral and medial base of first phalanx of each digit and lateral and medial sesamoid bones of each metatarsophalangeal joint.

REMARKS.—These muscles are relatively largest in *Eumops*. Their relationships are similar in all three genera.

ACTION.—Flexion of the digits.

CONCLUSIONS

Adaptations for Flight

The remarks below, based on the bats under consideration, probably apply at least to the microchiropteran families Molossidae, Vespertilionidae and Phyllostomidae.

Many types of flying animals have tended to develop body shapes that are aerodynamically favorable, bodies that neither create excessive amounts of drag nor counteract the lift developed by the flight surfaces. The short, dorsally arched and moderately flat

bodies of bats achieve this end surprisingly well. The occipital region of the head lies close to the inter-scapular region in bats and the head and body together are somewhat teardrop-shaped. This body form does not create undue amounts of drag while the bat is in flight. Because of its rounded dorsal surface and more nearly flat ventral surface, the body forms, together with the uropatagium, an airfoil from which some lift is obtained during flight. Because the bodies of most bats are more nearly flat than those of most birds, the bodies of bats are probably more effective as airfoils; that is to say, they develop relatively greater amounts of lift.

A tendency toward inflexibility of the vertebral column is evident in both bats and birds, being more strongly developed in the latter. A strong base to which the wings and flight muscles can attach is important in both of these groups. Some rigidity of the vertebral column is necessary in bats because powerful flight muscles that require strong, steady surfaces for attachment originate on the thoracic vertebrae and on the ribs. Furthermore, dorsoventral and lateral movements of the vertebral column while a bat is in flight affect the drag and lift created by the animal's body, the camber of the plagiopatagium, the tautness of this membrane, and to some extent the position of the uropatagium. During flight a bat maintains a fairly high energy output, and it is of advantage to the animal that the rigidity of the vertebral column is primarily the result of the structure of the vertebrae and not of muscular effort.

For the sake of aerodynamic stability of the animals and increased manageability of their appendages, there has been a trend in both bats and birds toward concentration of weight near the center of gravity. Various parts of the skeletal and muscular systems of the bats here considered have become specialized so as to effect a remarkable division of labor between the muscles, and at the same time to concentrate the responsibility for the most demanding jobs on the large muscles near the center of gravity. A locking device between articulating limb bones also commonly serves these ends in bats.

Several interesting examples are worthy of mention. The locking of the supraglenoid tuberosity of the scapula into the depression in the proximal end of the humerus tends to stop the extension of the humerus by relaying the force of the extension to the scapula. This transfers the burden of stopping the extension to the group

of powerful muscles that bind the scapula to the body and at the same time transfers the burden away from the relatively small M. teres major, M. latissimus dorsi, and the M. spinodeltoideus. During flight, when the M. spinodeltoideus is helping to elevate the wing during each upstroke, this muscle is probably relieved of the job of stopping the extension of the humerus and thus is given more time for rest between contractions. This extra recovery period probably is important when the wings are beating rapidly for fairly long periods of time. The locking of the greater tuberosity of the humerus against the scapula has been mentioned; this allows a longer recovery period for the pectoral muscles by making the posterior division of the M. serratus anterior responsible for stopping the upstroke, and probably also for starting the downstroke. Locking arrangements between bones occur also between the spinous process of the medial epicondyle of the humerus and the proximomedial part of the radius, between the distal epiphysis of the radius and the lunar, and between the trapezoid and the base of the second metacarpal. These locking devices all tend to stop mechanically the extension of some segment of the wing and transfer the force of that extension proximad to the heavy muscles attaching the scapula to the axial skeleton. This transfer obviates the need for distally situated musculature to stop the extension movement and also concentrates the weight of the animal near the center of gravity. Certain specializations of some of the forearm muscles also serve to achieve this weight concentration by making extension and flexion of the manus occur automatically with the corresponding movements of the forearm. Because their origins are slightly proximal to the lateral epicondyle of the humerus, the thin, largely tendinous Mm. extensor carpi radialis longus and brevis are stretched when the humerus is extended, thereby extending the digits. Much of the power necessary for the extension of the manus is thus transferred proximad to the triceps muscles. In *Eumops* and *Myotis* the origin of the M. flexor carpi ulnaris is on the long spinous process of the medial epicondyle of the humerus; flexion of the forearm by the M. biceps brachii stretches the M. flexor carpi ulnaris and automatically causes posterior flexion of the manus. In the course of the wing-beat cycle the manus is extended at the top of the upstroke and held rigid against the force of the airstream throughout the downstroke, and then is flexed at the start of the upstroke; most of the power necessary for the mentioned sequence of action probably is supplied

in the Molossidae and the Vespertilionidae by the Mm. triceps brachii and biceps brachii rather than by the muscles situated in the forearm. The limiting of the planes of movement at certain joints also serves to increase mechanical efficiency and concentrate the weight. The humeroradial, radiocarpal and carpometacarpal joints all limit movement in the anteroposterior plane. This limitation of movement enables the control of rotational stability, adduction and abduction, to be concentrated in the centrally located muscles that act on the humerus or proximal end of the radius.

Bats and birds have obviously met many of the problems of flight in different ways. A striking example of different specializations serving parallel functions is afforded by the muscles that control the wings. The trend in birds has been to concentrate all of the power for beating the wings in the pectoralis muscles, the pectoralis major causing the downstroke, and the pectoralis minor, the upstroke. The pectoral girdle in birds serves as a rigid base for the wings. The claviculae and coracoids are braced against the sternum and the scapulae are long, thin, bladelike structures that lie nearly immovably against the ribcage. Almost the reverse of this situation occurs in bats, in which an intricate division of labor has evolved between a number of muscles that control the wingbeat. Operation of this system is based upon the retention of a large, broad scapula, and a pectoral girdle that is nowhere attached immovably to the axial skeleton and that retains considerable mobility. The downstroke is controlled mostly by the M. pectoralis, the posterior division of the M. serratus anterior, and the M. subscapularis. The coracoid head of the M. biceps brachii also helps slightly in the downstroke in *Myotis* and *Macrotus*; in *Eumops* (and in all of the other genera of molossid bats that I have examined) this muscle is large and because of specializations of the coracoid process of the scapula helps considerably in the downstroke. The division of labor is possible because the scapula is moveable and has a large surface area. The scapula has become faceted; therefore its surface area is increased and it can provide origin for large flight muscles. Furthermore, the scapula is free to rock on its anteroposterior axis; thus, when the humerus is locked against the scapula at the top of the upstroke the anterior division of the M. serratus anterior can help in the wing-beat cycle by tipping the lateral edge of the scapula ventrad. The upstroke is powered by dorsally situated muscles, including the trapezius group, the deltoideus group, and the large

M. infraspinatus. Whereas the control of the wings is seemingly as effective in bats as in birds, the major flight muscles in bats are not all ventrally situated; hence, in terms of stability during flight, the weight distribution in bats is not so favorable as that in birds. To summarize: birds have a strongly braced and rigid pectoral girdle and the pectoralis muscles provide the power for both the upstroke and the downstroke of the wings; bats have a moveable scapula, and a group of muscles share the burden of controlling the wing-beat.

When the animals are in flight the actions of the large muscles controlling the wings seem to control the respiratory cycle in both bats and birds. During flight this is probably of major importance in connection with meeting the increased metabolic demands of the animals, and tends to put to use the force exerted on the ribcage by some of the powerful flight muscles. Because certain muscles that control the wings change the volume of the thoracic cavity in birds it is thought that the wing-beat and respiratory cycles in these animals are synchronized (Krogh, 1941, Zimmer, 1935). Authors have disagreed as to whether inspiration occurred during the upstroke and expiration during the downstroke or *vice versa*, but experimental work clearly has shown that, at least in flights of short duration in the domestic pigeon (*Columba livia*), inspiration is synchronous with the upstroke and expiration synchronous with the downstroke (Tomlinson and Kinnon, 1957). Judging by the hinging of the sternum and the actions of certain major flight muscles, an analogous situation probably obtains in bats. During the upstroke of the wings in bats the M. pectoralis and the posterior division of the M. serratus anterior are relaxed and the humerus is elevated by the abductors of the brachium. As the humerus rises the pectoralis muscle is stretched and tends to pull the post-manubrial part of the sternum dorsad and reduce the volume of the thoracic cavity. Towards the top of the upstroke, when the humerus locks against the scapula, the axillary border of the scapula is pulled upward and the posterior division of the serratus anterior is stretched, tending to pull the ribs dorsad and craniad, push the posterior segment of the sternum ventrad, and increase the volume of the thoracic cavity. When that muscle and the M. pectoralis are both stretched their actions on the ribcage partly counteract each other; but when the axillary edge of the scapula tips sharply upward at the top of the upstroke the effect of the serratus muscle probably overrides that of the pectoralis muscles and the ribcage expands.

At the top of the upstroke, if the posterior division of the M. serratus anterior contracts while the M. pectoralis is still relaxed (as may occur in the course of the usual wing-beat cycle) the force tending to expand the ribcage would increase further. After the downstroke is begun and the pectoralis muscles contract, the volume of the thoracic cavity is reduced by the upward force exerted against the post-manubrial part of the sternum and the direct pressure of the contracting muscles against the ribcage. Therefore, during the upper part of the upstroke and the start of the downstroke inspiration probably takes place, and expiration probably occurs during most of the downstroke. Without experimental evidence the exact time of inspiration in relation to the wing-beat cycle in bats can not be stated with certainty. The anatomical evidence strongly suggests, however, that in bats as in birds the rate of the wing-beat and the respiratory rate are in synchrony, and that expiration is simultaneous with the downstroke.

The hind limbs of bats, unlike those of birds, enter into the mechanical arrangement for flight by anchoring both the wing and interfemoral membranes. In order to function effectively in this capacity the hind limbs have a strikingly reptilian posture, in which the femur extends laterad at roughly right angles to the body. Owing to this posture, the range of movement of which the hind limbs are capable allows them to assume a position during flight that stretches the uropatagium and holds it in approximately the position of a bird's tail, whereas when bats crawl the shank is brought downward and forward and is oriented almost vertically to the substrate. The odd postures of the hind limbs of bats seem to be the result of the importance of these appendages in both aerial and terrestrial locomotion.

The Mechanics of Bat Flight

High-speed photographs show that the wing-beat cycle in bats closely resembles that in birds in terms of the movements performed. Many of those movements in bats were described by Eisentraut (1936). The downstroke is the power stroke; the wings are fully extended throughout the stroke and the direction of movement is downward and forward. The upstroke is the recovery stroke; the wings are partly folded during this phase, and the stroke is directed upward and backward. The deflection of the wings away from a direct up and down movement is due in part to the force of the air pressure against the wing membranes. The proximal segment of

the wing supplies most of the lift and the distal segment supplies the thrust developed by the wing-beat. Flight in bats and birds, then, is accomplished in nearly the same way; but the means by which the movements are achieved differ greatly.

At the beginning of the upstroke in bats the adductors of the humerus and the flexors and extensors of the radius relax and the forearm flexes slightly as a result of the tonus of the Mm. biceps brachii and triceps brachii, the automatic flexion of the manus by the stretched M. flexor carpi ulnaris (this automatic flexion does not occur in *Macrotus*), and the force of the air stream. Contraction of the abductor muscles of the brachium then raises and flexes the humerus while the distal parts of the limb are relaxed. The medial edge of the scapula is tipped ventrad by the trapezius muscles, and the humerus is elevated by the deltoideus group and the large M. infraspinatus muscle. The insertions of the deltoideus muscles and the M. infraspinatus are so situated that as they raise the wings they tend to rotate the leading edge upward and keep the distal part of the wing at a fairly high angle of attack. Accordingly, the wing surfaces produce some lift during this part of the cycle, and the airstream helps to lift the wing. The convex dorsal surfaces of the wings, and their partial flexion during the upstroke, reduce the drag created during the upstroke (Fig. 2, Pl. 3). The upstroke in the three bats studied by me is more rapid than the downstroke, as noted by Eisentraut (*op. cit.*) in *Myotis myotis, Rhinolophus hipposideros* and *Plecotus auritus,* and by Orr (1954: 206) in *Antrozous pallidus.* Although in terms of energy output the upstroke is less efficient in bats than in birds, the upstroke in bats probably requires only a fraction of the power demanded by the downstroke.

At the top of the upstroke the greater tuberosity of the humerus contacts the scapula and the force of the upstroke is transferred to this element. Because the vertebral border of the scapula has been tipped ventrad by the action of the trapezius muscles, the broad, thick posterior division of the M. serratus anterior (that inserts on the *axillary* border of the scapula) is stretched by the stage in the cycle at which the humerus locks against the scapula. The elastic effect of the tonus of the posterior division of the M. serratus anterior may stop the upstroke; or this muscle may contract as the humerus locks, thus stopping the stroke. In either event, contraction of this muscle, with the consequent pulling downward of the axillary border of the scapula and the resulting

adduction of the locked humerus, probably initiates the downstroke, with the help of the tonus of the stretched M. pectoralis. When the downstroke is started, the pectoralis muscles contract. Although it supplies the largest share of the power necessary for the downstroke, the M. pectoralis has considerable help in this action. The posterior division of the M. serratus anterior relieves the M. pectoralis of the burden of actively stopping the upstroke and starting the downstroke and assists the M. pectoralis through the upper part of the downstroke, while the humerus is still locked against the scapula. The serratus muscle can not act on the humerus when the greater tuberosity of the humerus loses contact with the scapula, but throughout the downstroke the M. pectoralis is helped by the large M. subscapularis (and in *Eumops*, and probably in all molossid bats, by the action of the large coracoid head of the M. biceps brachii). At the start of the downstroke the M. subscapularis and the Mm. triceps brachii and biceps brachii extend the humerus and the forearm. Extension of the forearm stretches the largely tendinous M. extensor carpi radialis longus and the M. extensor carpi radialis brevis, and the metacarpals are automatically extended. The digital extensors, with the aid of the force of air pressure beneath the chiropatagium, complete the extension of the chiropatagium. Thus, concurrent with the start of the downstroke, the forelimb is fully extended and the wing membranes are spread. Anteroposterior rigidity of the forearm and manus during the downstroke is controlled largely by the antagonistic actions of the flexors and extensors of the forearm, the Mm. biceps brachii and triceps brachii; rotational stability of the forelimb is maintained by the antagonistic actions of the M. pectoralis and the M. biceps brachii.

The camber and angle of attack of the distal segment of the wing is under the control of the rotators of the humerus, the flexors of the phalanges of digits three to five, and the angle of the dactylopatagium minus; but owing to the elasticity of the membranes, the flexibility of the bones of the digits, and the "give" that occurs at the interphalangeal joints, the camber is also controlled by changing air pressures. The distal segment of the wing supplies thrust during the downstroke, and to perform this function the distal flight surfaces must be able to have a different angle of attack during the downstroke than during the upstroke. The leading edge of the distal segment of the wing is formed by the second and third digits, and serves as a relatively rigid support

for the leading edge of the wing. The trailing edge of the wing has no such continuous support, and the force of air pressure during the downstroke tends to push the trailing edge and posterior parts of the chiropatagium upward and overcome the slight ventral flexion of the phalanges of the fourth digit. Because the distal parts of the chiropatagium are less strongly braced and are subjected to greater air pressures than the proximal parts, the "pitch" of the chiropatagium (like the pitch of some airplane propellers) increases distally, and the greatest part of the forward thrust seems to be supplied by the section of the chiropatagium between the third and the fourth digits.

In the proximal segment of the wing, the camber and angle of attack are influenced by the positions of the propatagium, the fifth digit, and the hind limbs. The humerus and radius form a relatively inflexible brace for the anterior edge of the proximal segment of the wing, whereas the trailing edge of this segment is unsupported, and its rigidity depends upon its being tautly stretched between the fifth digit and the hind limb. When the wing is extended the chiropatagium is pulled forward and held taut by the M. occipitopollicalis, and increases the area and camber of the proximal segment of the wing. The angle that the propatagium makes with the plagiopatagium seems to be fairly constant in a given species, but can be varied somewhat by flexion or extension of the thumb. Because the proximal segment of the wing produces most of the lift supplied by the flight membranes, that segment must retain roughly the same angle of attack throughout the downstroke in order to develop the maximum lift; this demands that the fifth digit be braced so as to withstand the force of air pressure on the underside of the wing during the downstroke phase of the wing-beat cycle. A number of remarkable specializations serve to make the fifth digit a relatively rigid anchor for the distal edge of the plagiopatagium. The fifth metacarpal is strongly built and is curved more strongly ventrad than are the other metacarpals (in *Eumops* it is laterally compressed). In addition, the fifth metacarpal is braced against upward pressures by the pisiform bone and the M. abductor pollicis longus and M. abductor digiti quinti. The hind limb forms the proximal anchor for the posterior part of the plagiopatagium, and is steadied during flight largely by the adductors and abductors of the femur and the flexors of the shank.

The hind limbs not only serve as proximal anchors for the plagiopatagium but govern the angle of attack of the uropatagium. The

position of the uropatagium has an important effect on the equilibrium of the body during flight. A slight raising (abduction) of the hind limbs with a consequent lifting of the uropatagium and tail attends the partial flexion of the forelimb and the beginning of the upstroke. Elevation of the uropatagium and tail continues throughout the upstroke of the wing; at the start of the downstroke, when the wings are fully extended, the hind limbs and uropatagium are higher than they are at any other part of the cycle. This up-and-down movement of the hind limbs compensates for the raising and lowering of the anterior parts of the wing membranes and tends to keep the angle of attack of these membranes fairly constant throughout the entire cycle. The proximal part of the anterior portion of the plagiopatagium is raised and lowered in relation to the body as the wings are raised and lowered. If the hind limbs, the places of anchorage of the proximal part of the posterior section of the plagiopatagium, were to be held in the same position relative to the body throughout the wing-beat cycle, the angle of attack of the plagiopatagium in parts of the cycle would be such that this membrane would not function efficiently as a lifting surface. With the uropatagium moving up and down in synchrony with the strokes of the wings, however, the angle of attack remains roughly the same throughout the wing-beat cycle. The dorsal movement of the hind limbs tends also to keep the body horizontally oriented during the wing-beat cycle by compensating for the changing position of the wings, which move from in front of the center of gravity of the animal at the bottom of the downstroke to behind the center of gravity at the top of the upstroke. The raising of the hind limbs during the upstroke pulls the uropatagium upward so much that it is at a low angle of attack and is developing but little lift. The posterior part of the animal is thus supported to a lesser extent than it is when the uropatagium angles downward, and the posterior part of the body tends to drop. At the same time that the uropatagium is developing a minimum of lift, the wings are extended at their posteriormost position, well behind the center of gravity of the body, and the anterior end of the body tends to "topple" frontward. As a result of the interplay of these two tendencies, the body stays on a fairly even keel. In the downstroke the function of the uropatagium is the same. As the wings are adducted in the downstroke the hind limbs and uropatagium are lowered until at the bottom of the stroke the uropatagium is at the highest angle of attack it attains in the wing-beat cycle. Again, the two important

functions—maintenance of a fairly constant angle of attack of the plagiopatagium and compensation for the changes of position of the lifting surfaces relative to the center of gravity—are performed. The hind limbs pull the trailing edge of the plagiopatagium ventrad as the leading edge is moved ventrad by the forelimb, and the angle of attack of the plagiopatagium remains nearly the same throughout the stroke. When the wings are near the bottom of the downstroke the uropatagium is at its greatest angle of attack and is developing maximum lift, tending to lift the posterior part of the body. The wings, at this point, are anterior to the center of gravity of the body and are tending to tip the anterior part of the body upward. This lifting of the anterior part of the body by the wings, then, is counteracted by the lifting of the posterior end of the body by the depressed uropatagium; accordingly, the body stays nearly horizontally oriented.

Orr (1954:206), studying *Antrozous pallidus*, noticed that the uropatagium was lowered with the downstroke and raised during the upstroke. He incorrectly, I think, concluded that the lift gained by the lowered uropatagium during the downstroke compensated for the loss of lift that occurs with the next upstroke.

In level flight the dorsal and ventral movements that the hind limbs, uropatagium and tail perform during the wing-beat cycle are clearly not the result of the legs being pulled up and down by intermittent contractions of the femoral abductors and adductors. The hind limbs are held in their flight-position by the tonus, or by weak contractions of the muscles of these appendages, and instead of moving the hind limbs with each wing stroke the muscles tend to hold the limbs steady. The tail also is held in a fairly constant position. As the wing is elevated and lowered, however, the amount and direction of the pull exerted by the wing-membranes on the limb varies, due to the variation in the dorsoventral position of the wings, the force of air pressure against the membranes, and the degree of extension of the wing. Accordingly, the force of the pull on the hind limbs varies in the upstroke from a downward pull during the lower part, to a weak lateral pull during the middle part, to a dorsal pull during the upper part, and the hind limbs and uropatagium are pulled progressively higher throughout the stroke by the wing membranes. In the downstroke the pull on the hind limbs changes from a strong dorsolateral pull during the upper part of the stroke, to a strong lateral pull during the middle part, to a strong ventrolateral pull during the lower part, and the hind

limbs are forced progressively lower during the stroke. The differences in the positions of the hind limbs, uropatagium and tail at the different points of the wing-beat cycle, then, are the result of the changes in the strength and direction of pull of the wing membranes acting against the muscles of the hind limb that tend to hold the limbs rigid. In deviations from level flight, of course, the muscles of the hind limbs often effect changes in the position of the uropatagium.

Comparisons of the Bats Studied

It is worth-while to re-examine some of the differences between the three bats under consideration with the aim of learning which modifications are more efficient adaptations to the basic chiropteran mode of life. The kind of character here called "advanced" is one that makes the bat a more effective flying animal. Modifications that enable bats to occupy special environmental niches are regarded as specializations, whereas modifications that enable the animals to fly more efficiently, no matter what particular type of flight they use, are termed advanced characters.

The obvious differences between the sterna of the three genera under study seem in part to be the result of the roosting habits of these animals. Relative to the length of the thoracolumbar section of the vertebral column, the sternum is longest in *Eumops* and shortest in *Macrotus*. As an additional contrast, the sternum of *Eumops* has almost no keel, and that of *Macrotus* bears a large keel. The crevice roosting habit of *Eumops* makes an increase in the depth (dorsoventral thickness) of the body disadvantageous, yet the strong flight characteristic of this genus demands powerful musculature. Thus, the long, unkeeled sternum serves to give a large surface for the attachment of the pectoralis muscles without increasing greatly the depth of the body. Because *Macrotus* roosts exclusively by hanging, there probably is no selective pressure exerted against the development of a deep body and it is understandable that the area needed for the attachment of the pectoral muscles is provided by the short, keeled sternum. In *Eumops*, because of the shape of the sternum, the pectoralis muscles have a long, thin origin. In body shape *Myotis* is roughly intermediate between *Eumops* and *Macrotus*. *Myotis* has a short deep manubrium and the posterior part of the sternum has a low ridge. This genus roosts both by hanging, in company with other individuals of its kind, and by wedging itself into small holes or fissures. Per-

haps because of its small size and more generalized roosting habits, a shallow body is not so important in *Myotis* as in *Eumops*. In any case, the shape of the sternum seems not to be a character clearly indicative of degree of advancement in bats, and is strongly influenced by the roosting habits of the animals.

The differences between the scapulae of the three bats may also result in part from differences in roosting habits. Probably because there has been less selective pressure against the development of a deep thorax in bats that roost by hanging than in crevice-dwelling bats, *Macrotus* has developed the M. pectoralis to an extent not found in the other genera. As a result, there has been no need for the perfection of an effective division of labor between several flight muscles to limit the size of the M. pectoralis in *Macrotus*, and the scapula has not been so specialized to serve as a place of origin for some of the auxiliary flight muscles in *Macrotus* as it has in the other genera. In the crevice-dwelling *Eumops* dorsoventral thinness would seem to be advantageous and the scapula is highly specialized to give origin to the muscles aiding the M. pectoralis in the downstroke. Such characters as the elongation of the scapula, sharp downward angle of its supraspinous part, large anterior flange on the anterior rim of the supraspinous fossa, and medially projecting coracoid process indicate this adaptation to provide larger area for insertion of muscles aiding the pectoralis muscles. *Myotis* has some of these specializations of the scapula (for example large anterior flange on rim of supraspinous fossa) but in general is not so specialized in this regard as *Eumops*. Although specialization of the scapula is characteristic of most groups of the suborder Microchiroptera, selective pressure influencing development of a specialized scapula varies according to roosting habit and kind of flight of the bats. Nonetheless, because specializations of the scapula in bats seem to indicate a more efficient utilization of the mechanical scheme for flight based upon a movable scapula and heavy musculature attaching this element to the axial skeleton, these specializations are regarded as advanced characters.

Crevice-dwelling seems to favor the specialization of the humeroscapular locking device. A firm lock is one detail of the chiropteran shoulder joint seemingly highly efficient for flight. Accordingly, enlargement of the greater tuberosity of the humerus and consequent locking of the humeroscapular articulation at a lower point in the upstroke is considered as an indication of advancement.

A few other characters indicative of advancement in bats can be

enumerated. Limitation of movement to the anteroposterior plane at the elbow, wrist and carpometacarpal joints is necessary for the limb to serve as an effective framework for the flight surfaces. Thus, modifications that tend to brace these joints are advanced characters. Centralization of weight is another important trend toward aerodynamic efficiency. The locking devices that limit the extension of the segments of the forelimb, and the specializations of the Mm. extensor carpi radialis longus and brevis and the M. flexor carpi ulnaris that allow these muscles to operate as elastic cords that automatically move the manus with movements of the forearm serve this end, and are therefore advanced characters. The fifth digit, together with the hind limbs, has the important function of controlling the angle of attack of the plagiopatagium, which is the main lifting surface of the flight membranes. Specializations that strengthen the fifth metacarpal and modifications that enable other bones or muscles to brace the fifth digit, then, represent advanced characters.

Eumops has developed all of the advanced characters mentioned above to the highest degree of any of the three genera under study. *Myotis* exhibits many of these characters, but they are less perfectly developed than in *Eumops*. *Macrotus* is the least advanced. Its scapula, proximal end of the humerus and joints of the forelimbs are far less advanced than those of the other two genera. The M. flexor carpi ulnaris does not serve to flex the manus automatically when the forearm is flexed as this muscle does in the other genera. The fifth digit is slightly more strongly braced in *Macrotus* than in *Myotis*, but is not nearly so well braced as in *Eumops*. On the basis of the few post-cranial characters assumed to indicate advancement within the suborder Microchiroptera, *Eumops* (Molossidae) is judged to be the most advanced and *Macrotus* (Phyllostomidae) is the least advanced; *Myotis* (Vespertilionidae) is intermediate. I have examined additional members of each of the families represented by these bats, and judge that with respect to advancement the families should be listed as above. This is in agreement with Miller's (1907) currently accepted arrangement of these families.

Evolutionary Considerations

The fossil record of bats is scanty, and the stages represented by the record seem to be well above the level at which the bats diverged from their ancestral stock. The earliest undoubted chiropteran fossils are from the middle Eocene of Europe and North America, but even those bats were not extremely primitive; already

the basic chiropteran morphological pattern was established and certain refinements are evident. In *Palaeochiropteryx* from the middle Eocene of Europe, for example, the calcar is present, and in the manus the pollex bears the only ungual phalanx. Bats must have undergone their initial evolutionary development in the Paleocene or earlier.

Without a background of fossil material a study of the morphology of Recent bats can not certainly reveal their phylogeny. Nevertheless, the morphology of Recent bats suggests something of the early stages of evolution of the Chiroptera.

Before considering the evolution of bats it should be stressed that the modifications of the pectoral and pelvic girdles in these animals have been influenced strongly by the dual use of both the forelimbs and the hind limbs. Although aerial locomotion has greatly affected the evolution of the appendages of bats, some type of terrestrial locomotion in which the forelimbs are used is important in most bats. Consequently, natural selection may have operated against anatomical modifications that tended to make the forelimbs useless in terrestrial locomotion, even if such changes would have made these limbs more efficient in flight; thus, the evolution of the forelimbs has taken place within the limits imposed by the use of these appendages in terrestrial locomotion. In the same way, the evolution of the hind limbs, although influenced by the use of these limbs in terrestrial locomotion, has been partly controlled by the importance of these appendages as anchors for the wing membranes during flight.

Judging completely on the basis of the morphology of Recent bats, it seems that when bats were diverging from their insectivore progenitors—when the basic adaptations for flight were being developed—bats usually sought diurnal refuge in narrow, crevicelike retreats. Several lines of evidence support this idea.

The whole scheme of muscular and osteological specialization that enables bats to perform the downstroke (powerstroke) of the wings effectively may have resulted from a tendency, which probably originated due to the crevice-dwelling habits of early bats, to avoid dorsoventral thickening of the body. In no known bat has the M. pectoralis or the keel of the sternum developed to anything approaching the degree seen in most birds. The division of labor between the major flight muscles in bats has kept the size of the pectoralis muscles at a minimum, while tending to create a broad and moderately flat body that contrasts with a deep, fairly narrow body of most birds. Although the bodies of bats may serve as more

effective airfoils than those of birds, the weight distribution in bats is not so favorable to equilibrium during flight as is that of birds. In addition, because of the directions of the muscle pulls involved, adaptations enabling bats to retain a flat body seem not to develop strong muscular control of the wings so directly as is seen in birds. Seemingly, the primary advantage of the chiropteran body-shape is that it allows the bats to fit in small spaces. Clearly, to a crevice-dwelling bat a deep thorax would be a decided disadvantage, for it would greatly restrict the number of suitable roosting sites and would make locomotion within the crevice difficult. The moderately small pectoralis muscles, the relatively slightly keeled sternum, and the specializations creating a division of labor between several muscles that control the downstroke may result from bats having perfected flight while they were restricted to roosting in crevices, a niche that would have brought strong selective pressure to bear against the avian method of solving the problem of the muscular control of wings.

The posture of the hind limbs and forelimbs and the modifications of the pectoral and pelvic girdles in bats favor both the use of the appendages to support flight surfaces (this function demanding that the limbs be held out laterally from the body) and the operation of these limbs in connection with crawling within narrow spaces. Locomotion within a crevice can be especially effectively accomplished by an animal the limbs of which are directed mostly laterad instead of being oriented vertically to the substrate. In animals in which the flight surfaces consisted of membranes stretched between the limbs, both the crevice-roosting habit and the development of flight would have tended to force the development (or retention) of the posture of limb typical of bats today. At the critical early period in which flight in bats developed, the rate of evolution conceivably was increased if both the roosting habits and the foraging habits of the animals made the same general type of limb posture advantageous.

A crevicelike retreat is one that was probably more nearly ubiquitous during the early stages of the evolution of bats than any other kind of shelter. Although caves are popularly considered as the favored roosting places of bats, in many regions today where bats are known to be abundant, both in total numbers and in diversity of species, there are no caves and most of the bats seek refuge in some crevicelike retreat. The initial radiation of the

chiroptera would probably have been favored by the habit of occupying crevices.

The Recent chiropteran fauna includes many species, and several families, that roost exclusively by hanging pendant from some supporting surface and that are specialized in various ways to exploit successfully this roosting niche; characteristically these bats have shorter bodies and deeper chests, relatively large pectoralis muscles and less advanced scapulae and humeri than crevice-dwelling kinds. In bats that roost in crevices and those that roost by hanging the basic pattern of muscular control of the wings seems to be the same, but selective pressure has seemingly not favored the perfection of some of the major chiropteran adaptations to the extent in bats that hang that it has in crevice-dwelling bats. The post-cranial skeletons of certain representatives of the cave-roosting families Phyllostomidae and Rhinolophidae, and the mainly crevice-dwelling families Vespertilionidae and Molossidae were examined. Without exception, the crevice-dwellers have more nearly flat bodies and more advanced "chiropteran" adaptations for flight. Assuming that bats underwent their early evolution when they were crevice-dwellers, it seems that certain groups changed their roosting habits at a time when the major bat specializations of the pectoral girdle had not yet been perfected, and that because these animals were relieved of the selective pressure against the development of deep thoraces the pectoral girdle has not become so advanced (in terms of the chiropteran type of adaptation), and that the division of labor between the flight muscles has not developed to the extent found in present day crevice-dwellers. In any case, the differences between the post-cranial morphology of such cave roosting groups as the Phyllostomidae and the Rhinolophidae and the largely crevice-dwelling Molossidae indicate that the crevice-dwelling habit favors the development of the advanced "chiropteran" pectoral girdle.

Eumops is known to seek diurnal refuge in crevices and clearly is an advanced bat. Its highly developed humeroscapular locking device and the morphology of the scapula reflect an advanced degree of development of the division of labor between the flight muscles. These features and the long slender wing in *Eumops* may be responses principally to a "need" for rapid and prolonged flight and secondarily responses to a "need" for more efficient locomotion within a narrow space; some of the adaptations that favor rapid crawling within a crevice also favor the evolution of a long, high-aspect-ratio wing. The second digit, the third and fourth meta-

carpals and the fifth digit are all approximately the length of the forearm, and the phalanges of the third and fourth digits fold accordion-fashion against their respective metacarpals. This arrangement allows the wing to fold into a compact bundle that is manageable when the bat is crawling rapidly in a crevice. Also, this arrangement allows a long distal segment of the wing to be developed, for the phalanges of digits three and four fold back against the metacarpals and do not project awkwardly beyond the proximal end of the radius when the wing is folded as in non-molossid bats. The shallow body and fairly flat head of the mastiff bat not only suit the bat for crevice dwelling but improve the airfoil formed by the head, body and uropatagium. In the case of *Eumops,* then, some of the animal's most advanced characters, as well as certain remarkable specializations, seem to have developed within the limits imposed by the crevice-roosting habit. Conceivably the development of these characters may actually have been hastened by the selective pressure resulting from this habit.

It is evident that many of the major adaptations for flight differ in bats and birds, and it seems that the basic chiropteran muscular and osteological adaptations for flight are the result of bats having been crevice-dwellers during the period of their early evolution.

SUMMARY

A comparative study was made of the functional morphology of three North American bats, the western mastiff bat (*Eumops perotis* of the family Molossidae), the cave myotis (*Myotis velifer* of the family Vespertilionidae), and the leaf-nosed bat (*Macrotus californicus* of the family Phyllostomidae). The myology and osteology of the pectoral and pelvic girdles and their appendages was described, and remarks were made on the actions of the muscles. As a basis for functional considerations, a field study on the foraging and roosting habits of these bats was made in the desert and coastal regions of southern California in the summers of 1953, 1954, and 1957. Additional information was gained from high-speed photographs and observations of these bats in the laboratory.

All three of the bats here considered are insectivorous, but their roosting and foraging habits differ, as do their modes of flight and terrestrial locomotion. *Eumops* seeks daytime refuge chiefly in crevices or fissures in cliffs or large boulders, and roosting-sites are usually high above the ground. This bat is fairly active in its roost at various times of the day, and can crawl rapidly. The method

by which this bat crawls is remarkably effective within the narrow confines of a crevicelike retreat. *Eumops* is a speedy and enduring flier, but is unable to take flight from a level surface and must launch itself from at least six feet above the ground to attain sustained flight. In summer this bat forages continuously for roughly six and one half hours per night. Generally the nightly exodus from the roost begins about one hour after sunset and the bats return between one and two hours before sunrise. Mastiff bats usually forage high above the ground; their foraging range is at least five miles, and under certain conditions may be fifteen miles or more.

Myotis velifer seems to prefer caves for daytime roosting, but inhabits also buildings, and crevices and small holes in rocks. This bat usually roosts in clusters by congregating on ceilings or in crevices in ceilings of caves. The cave myotis can crawl fairly rapidly, although not with the speed or agility of *Eumops*. The flight of *M. velifer* is direct for a small bat, but when it chases insects its flight is erratic and highly maneuverable. Often it forages in riparian situations or over dry desert washes supporting scattered large plants; then it usually flies six to 15 feet above the ground. In the evening this bat generally emerges from its roost roughly one half hour after sunset, and seems to have but one major foraging period per night; each bat probably is on the wing no more than one and a half hours per night.

The leaf-nosed bat rests in the daytime almost exclusively in caves, and roosts by hanging from the ceiling with the body pendant and only the feet in contact with the rock. Terrestrial locomotion is confined to a unique kind of "walking" across a ceiling; *Macrotus* is incapable of crawling. The flight is slow and extremely maneuverable, and the animal is able to hover for several seconds at a time. In alighting, *Macrotus* performs a half roll and grasps the ceiling with its feet. It usually forages within three feet of the ground, and seemingly most of the prey is captured on the ground or is picked from vegetation. There is one pre-midnight and one early-morning foraging period, and each bat probably is on the wing less than one hour and forty-five minutes per night.

Between the three bats studied here considerable variation occurs in the aerodynamic characteristics of the flight surfaces, these differences reflecting mostly the foraging habits of the animals. *Eumops* has a long, narrow, high-aspect-ratio wing; the wing loading is higher and the camber is lower than in the other bats. In

general, the wings of *Eumops* are well adapted for rapid, prolonged flight. The wings of *Myotis velifer* are short, fairly broad and of high camber, and are adapted to develop high lift at low speeds. The wing loading is lower and the uropatagium is larger than in the other two bats, these characteristics favoring maneuverability. The wings of *Macrotus californicus* have approximately the same aerodynamic characteristics as those of *Myotis velifer,* but the uropatagium is smaller in the former. *Macrotus* probably owes its maneuverable flight in large part to specialization of its sensory equipment.

In bats the pectoral and pelvic girdles are highly modified for support and for control of the flight membranes. In the bats here considered the sternum of *Macrotus* is the only one having a keel, but in all three bats the joint between the manubrium and the body of the sternum allows the post-manubrial part of the sternum to swing ventrad; this arrangement probably puts the breathing cycle during flight partly under control of the major adductors of the wing. The scapula is large and faceted and provides a large area for muscle attachment. There are locking devices formed by the articulating elements at the scapulohumeral, the humeroradial, the radiocarpal, and the carpometacarpal joints; these joints mechanically stop the extension of the various segments of the forelimb. Because of specializations of the articular surfaces involved, flexion and extension of the forearm and hand can occur only in the anteroposterior plane. Many of the osteological and myological specializations of the pectoral girdle serve to transfer responsibility for control of the wings to muscles situated near the center of gravity of the animal. Such adaptations tend to increase the manageability of the forelimb and effect an advantageous weight distribution in terms of aerodynamic stability. The hind limbs have a reptilian posture in bats and are held more or less out to the sides of the body; several of the largest muscles in the pelvic girdle seem to function most importantly to steady the hind limbs and uropatagium during flight.

Although there are parallel trends toward rigidity of the vertebral column and centralization of weight in bats and birds, many of the basic adaptations enabling these animals to control their flight surfaces are different. In birds the pectoral girdle is braced rigidly against the axial skeleton and the power for the wing-beat is supplied almost entirely by the pectoralis muscles. Nearly the opposite mechanical arrangement obtains in bats, for in this group the

job of controlling the wing-beat is divided between a number of muscles, and this division of labor is possible mainly because of a large and moveable scapula.

In chiropteran flight the proximal segment of the wing (plagiopatagium and propatagium) supplies the lift and the distal segment of the wing (chiropatagium) supplies the forward thrust during the wing-beat cycle. The downstroke is directed forward and downward and is mainly under the control of the M. pectoralis, the anterior division of the M. serratus anterior, and the M. subscapularis; the upstroke is an upward and backward movement and is controlled principally by the trapezius and deltoideus groups of muscles. The proximal segment of the wing is stretched between the hind limb and the fifth digit. The hind limb is steadied mostly by the adductors and abductors of the femur and the flexors of the shank. As a result of a number of osteological and myological specializations the fifth digit is braced against the force of air pressure during the downstroke and maintains the plagiopatagium at a fairly constant angle of attack during this phase of the wing-beat cycle. The head, body and uropatagium form a crude airfoil that develops lift during flight. The uropatagium moves up and down with corresponding movements of the wings; during flight these changes in the angle of attack of the uropatagium change the amount of lift developed by this membrane and serve to keep the plagiopatagium at a fairly constant angle of attack and compensate for the changes of position of the wings relative to the center of gravity of the animal.

The assemblage of muscular and osteological specializations for flight characteristic of microchiropteran bats has resulted in these animals having broad, moderately flat bodies. This body-form suggests that in the time during which bats underwent their early evolution they were crevice dwellers, and that selective pressure operated against the development of the deep-chested body-form typical of birds. Because the demands of flight and of locomotion within a crevice favor the development of the kind of limb posture occurring in most bats, it is conceivable that the rate of evolution of these animals was increased by an early predilection for crevice-dwelling.

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FIG. 1. View of terrain which offers suitable roosting places for *Eumops perotis*. The domelike boulder of granodiorite on the left has several crevices in which *E. perotis* roosts in the daytime. Photo August 28, 1957, three miles northeast Perris, California.

FIG. 2. Closeup of part of the boulder shown in Fig. 1. The crevice in the lower left was usually occupied by a single *Eumops perotis;* the crevice beneath the tongue-shaped slab of rock in the upper right generally harbored three to six individuals.

FIG. 1. View of an oxbow in the floodplain of the Colorado River where *Myotis velifer* and *Macrotus californicus* forage. Such riparian situations provide optimal foraging habitat for *Myotis velifer* in the Riverside Mountains area. The strip of vegetation on the left is mostly tamarisk and screw bean; cattails border the water and some arrowweed are in the foreground. Photo August 22, 1957, 35 miles north and two miles east Blythe, Riverside County, southeastern California.

FIG. 2. View looking south across a small desert wash to the Riverside Mountains. The wash is a preferred foraging habitat of *Macrotus californicus; Myotis velifer* also forages there. Photo August 21, 1957, 36 miles north Blythe, California.

PLATE 3

FIG. 1. *Macrotus californicus* hanging from ceiling of cave. Note that leg by which animal hangs is extended nearly straight behind the bat. Photo June 29, 1954, 35 miles north Blythe, California. × ⅗.

FIG. 2. *Macrotus californicus* in slow, nearly hovering flight, with the uropatagium lowered. The wings are in the middle of the upstroke. Note the high camber of the right wing due to flexion of phalanges of the fifth digit. Photo June 29, 1954, 35 miles north Blythe, California. × ⅓.

FIG. 3. *Macrotus californicus* in level flight. The wings are at the top of the upstroke, but the digits have not yet been fully extended. Note that at this point in the wing-beat cycle the hind limbs extend almost directly behind bat and that camber of wings is reduced by extension of phalanges of fifth digit. Photo June 29, 1954, 35 miles north Blythe, California. × ½.

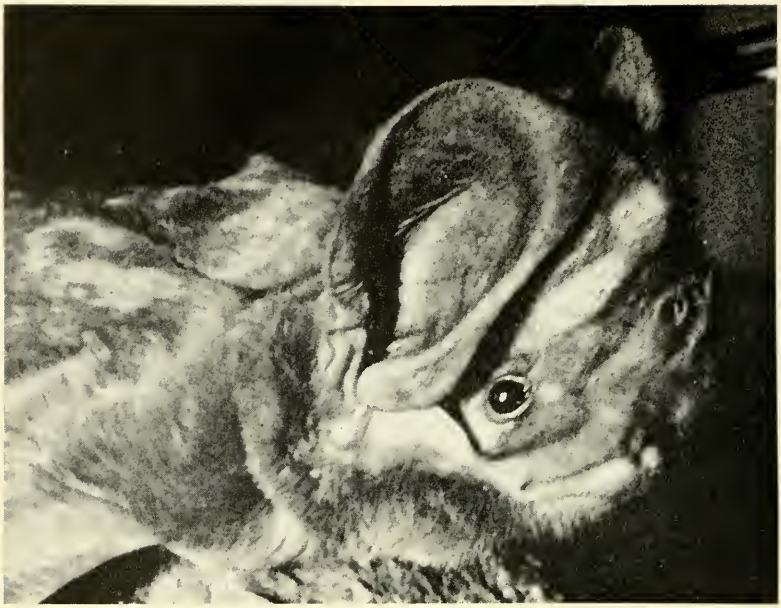

FIG. 1. Head of *Eumops perotis*, female, from two miles east of El Cajon, California, June 23, 1954, showing the position in which the ears are held when the animal is using its eyes. × 1⅓.

FIGS. 2 and 3. Same individual as shown in Fig. 1. 2) Front view, of bat crawling. Note that the right forelimb, which is in the middle of the forward component of the stride, is parallel to the substrate. 3) Side view of bat crawling rapidly. The forelimb is near the end of its forward movement; the hind limb is near the end of the propulsion part of the stride. × ⅔.

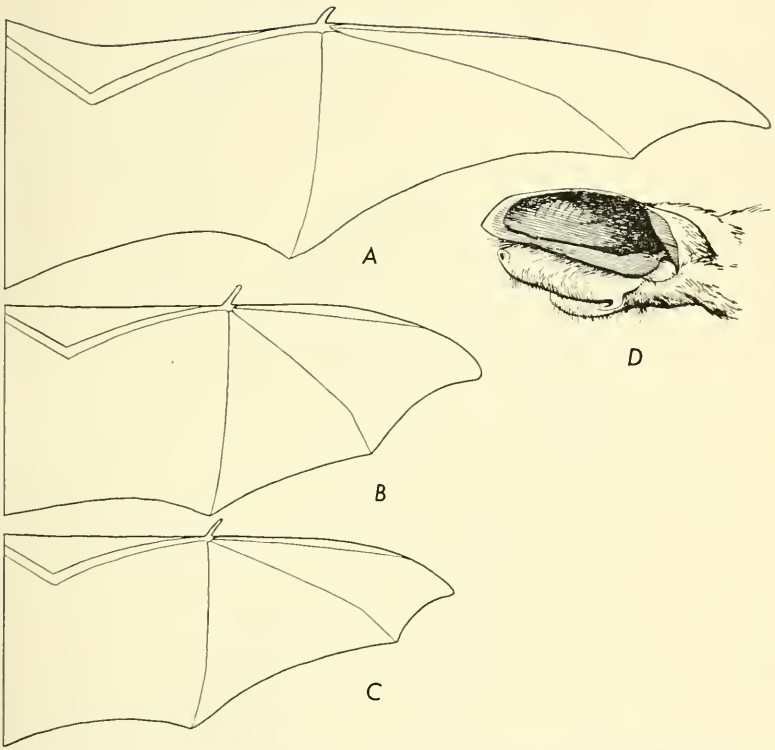

FIG. 1. Wings: *Eumops* (A), $\times \frac{1}{5}$; *Macrotus* (B), $\times \frac{1}{2}$; *Myotis* (C), $\times \frac{1}{2}$. Side view of the head of *Eumops* (D), $\times \frac{1}{2}$, showing the position of the ear during flight.

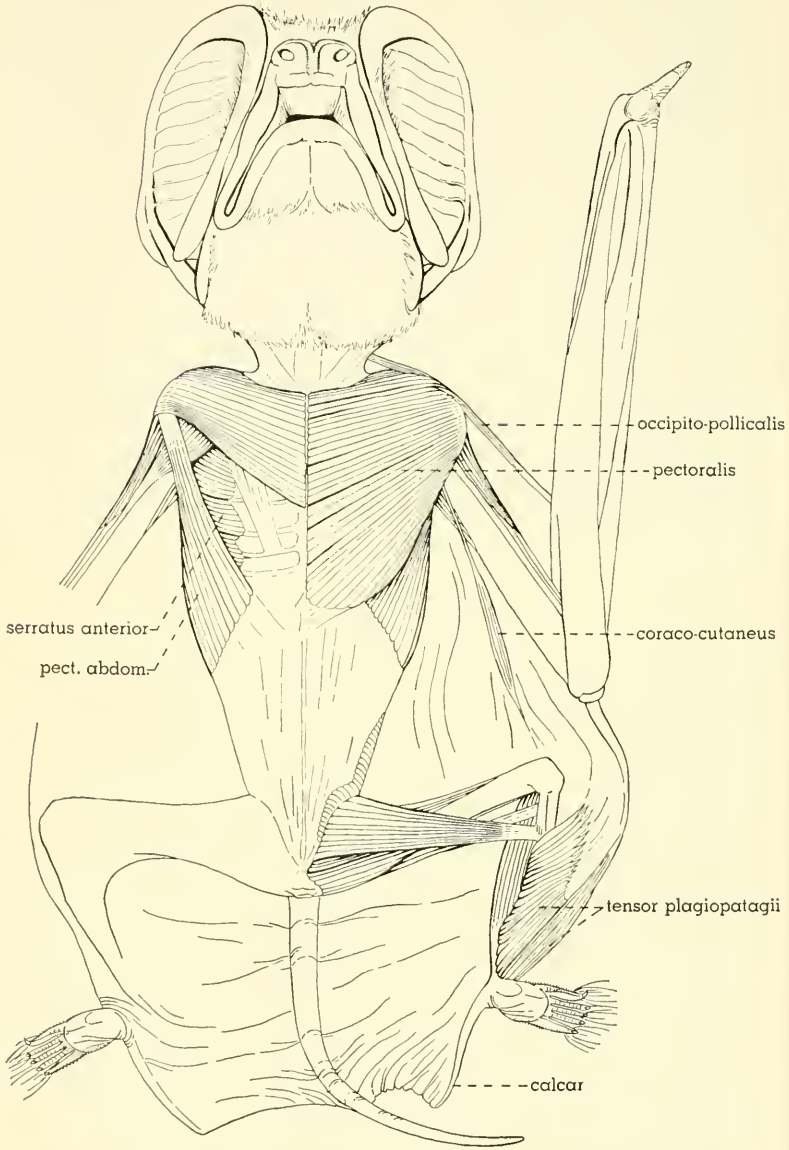

FIG. 2. Ventral view of *Eumops*, showing the proportions of the body and certain muscles, × 1.

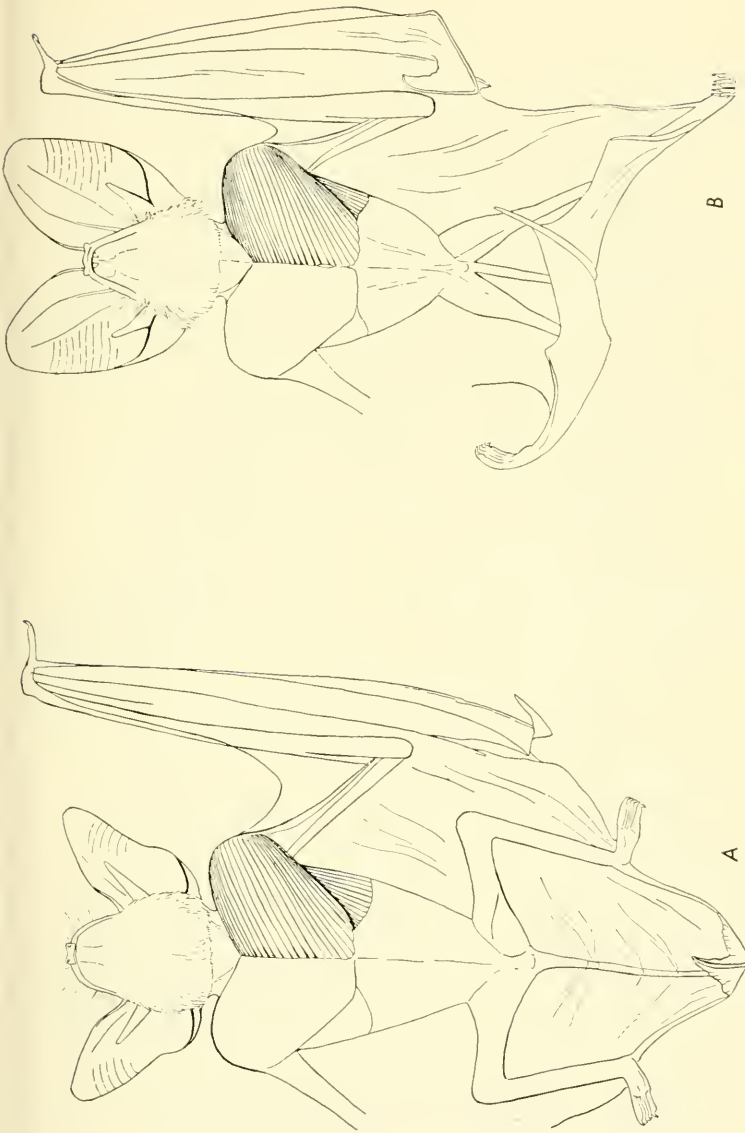

FIG. 3. Ventral view, showing proportions of the body and also two muscles (see fig. 2), of *Myotis* (A), × 1½, and *Macrotus* (B), × ⅔.

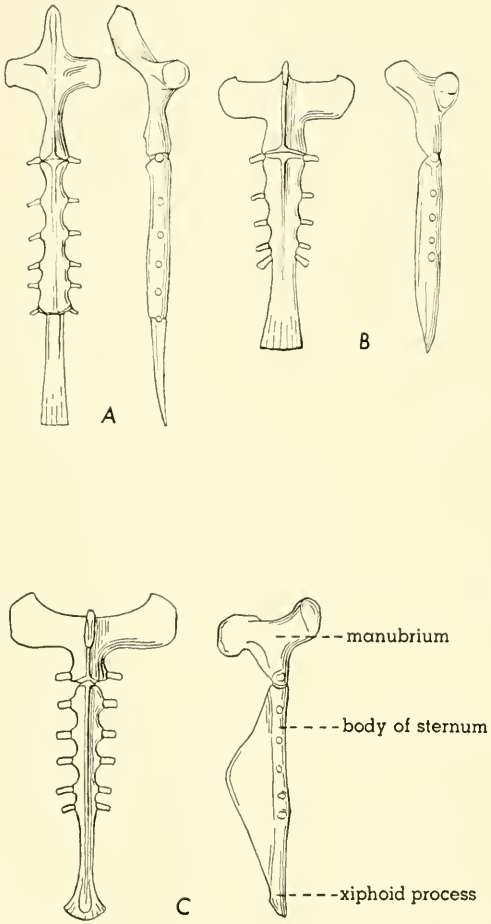

FIG. 4. Sternum: *Eumops* (A), × 2; *Myotis* (B), × 4; *Macrotus* (C), × 3. For each sternum the ventral view is on the left and the lateral view, on the right.

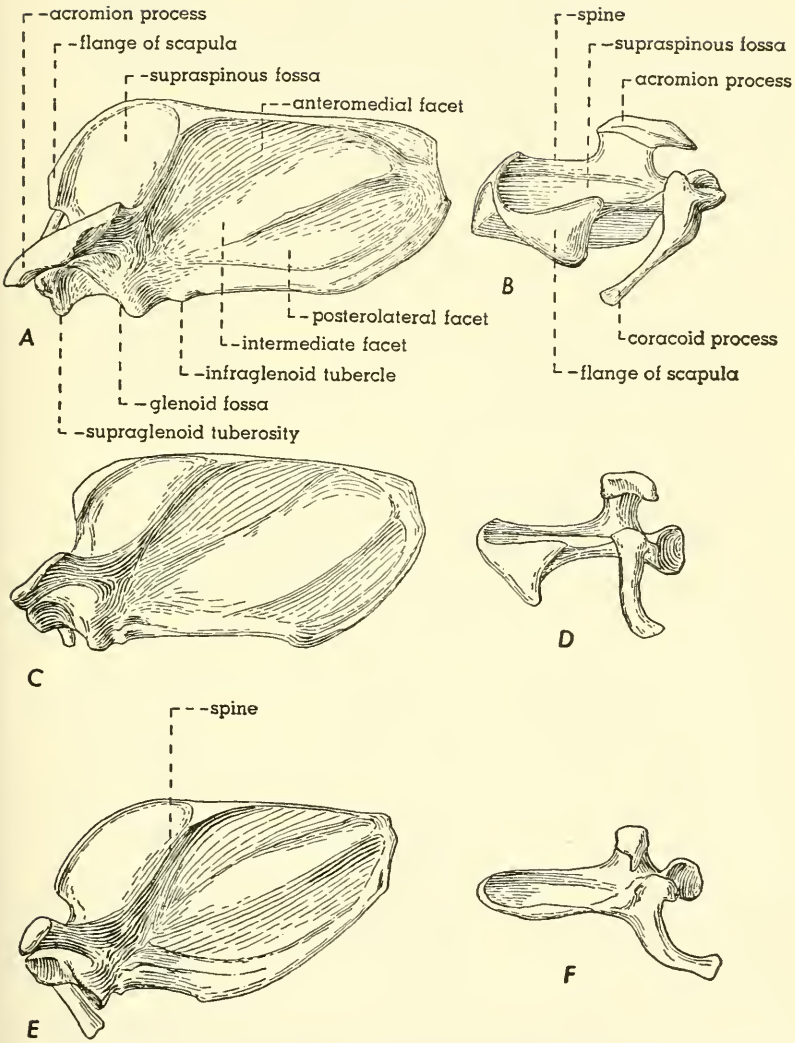

FIG. 5. Dorsal view and anterior view, respectively, of the left scapula: *Eumops* (A, B), × 2½; *Myotis* (C, D), × 5; *Macrotus* (E, F), × 4.

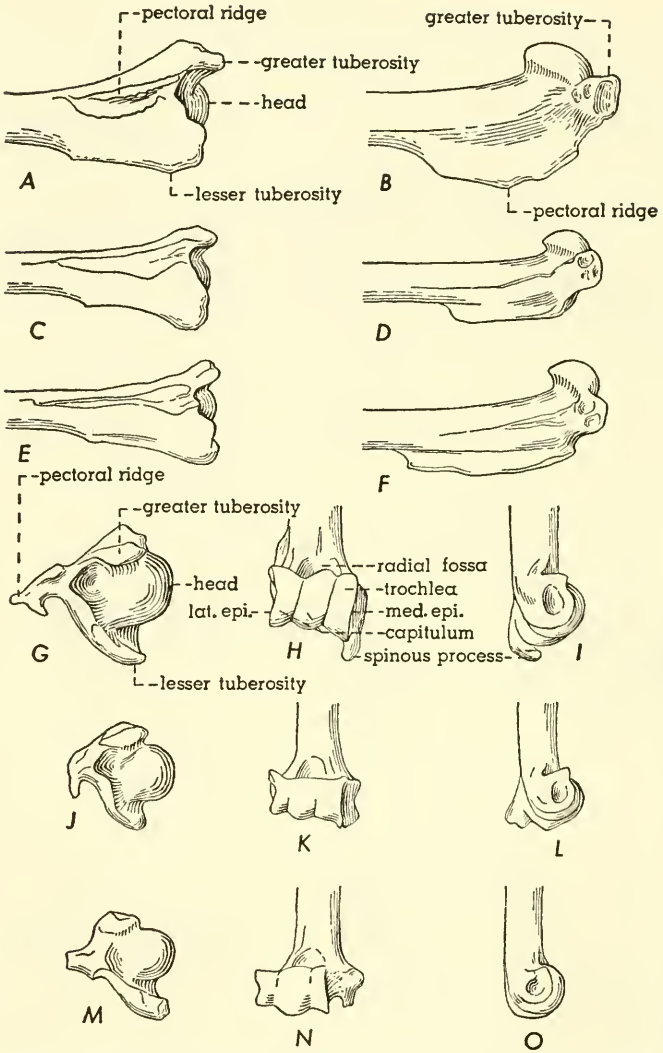

FIG. 6. Anterior and lateral view, respectively, of the proximal end of the right humerus: *Eumops* (A, B), × 3; *Myotis* (C, D), × 5; *Macrotus* (E, F), × 4. End view of the proximal end of the humerus: *Eumops* (G), × 3; *Myotis* (J), × 5; *Macrotus* (M), × 4. Anterior view and lateral view, respectively, of the distal end of the humerus: *Eumops* (H, I), × 3; *Myotis* (K, L), × 5; *Macrotus* (N, O), × 4. Med. epi.—medial epicondyle; lat. epi.—lateral epicondyle.

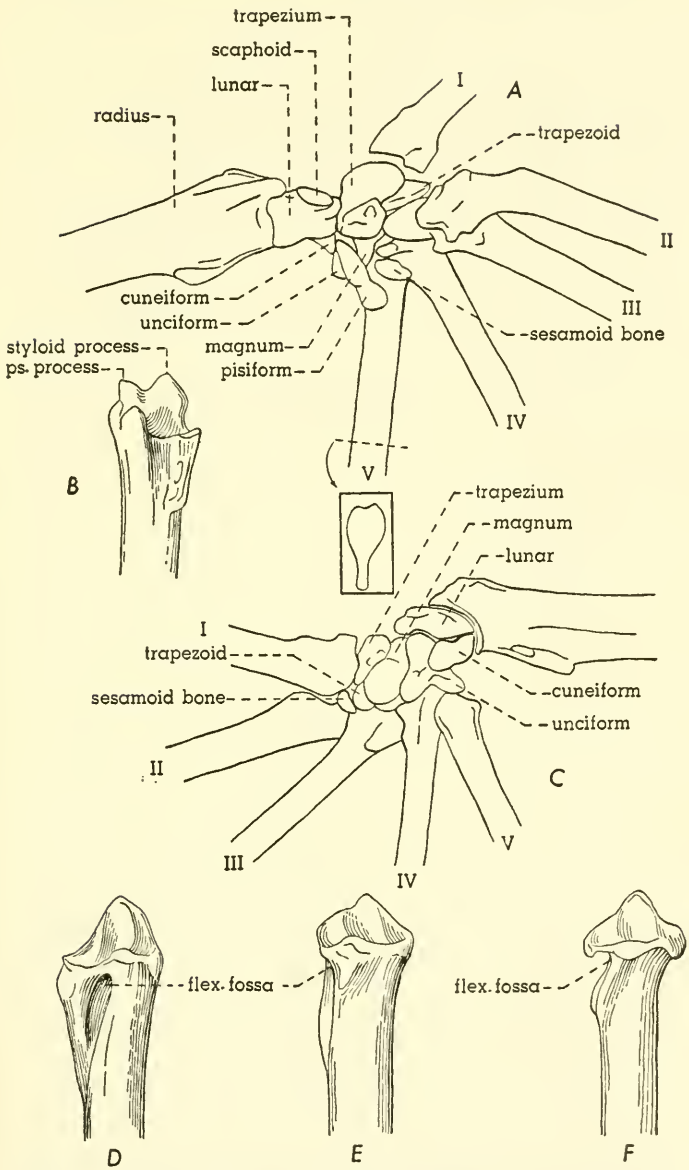

FIG. 7. Ventral view of the carpus of *Eumops* (A), × 4. Posterior view of the distal end of the left radius of *Eumops* (B), × 4. Dorsal view of the left carpus of *Eumops* (C), × 4. Anterior views of the proximal ends of the left radii: *Eumops* (D), × 4; *Myotis* (E), × 7; *Macrotus* (F), × 5. Inset shows cross section of the fifth metacarpal of *Eumops*, × 4. Flex. fossa—the depression into which the tendons of the Mm. biceps brachii and brachialis insert. Ps. process—pseudostyloid process.

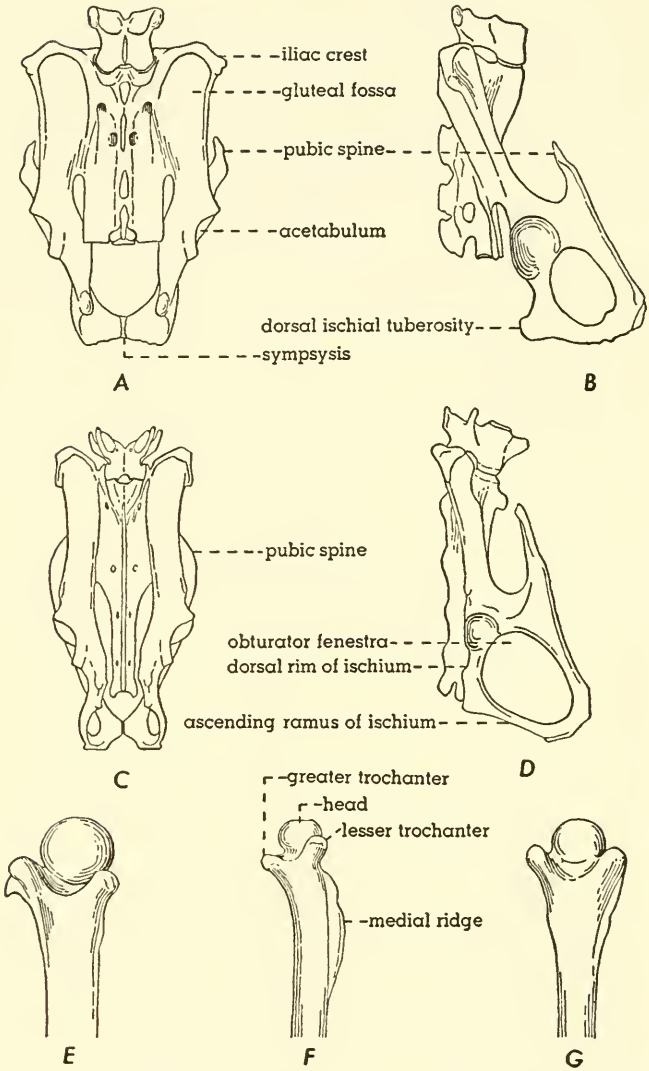

FIG. 8. Dorsal and lateral views, respectively, of the pelvis: *Eumops* (A, B), × 2; *Macrotus* (C, D), × 4. Posterior view of the proximal end of the left femur: *Eumops* (D), × 4; *Myotis* (E), × 5; *Macrotus* (F), × 7.

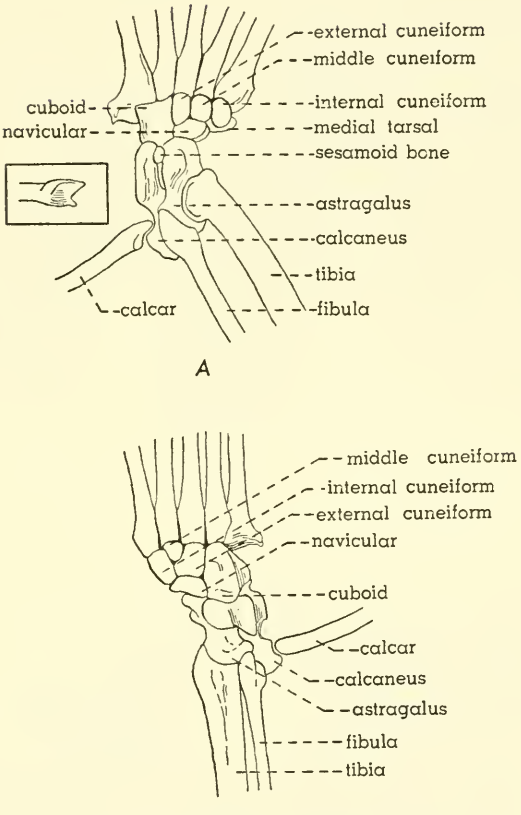

FIG. 9. Dorsal view of the left tarsus of *Eumops* (A), × 5; and the right tarsus of *Macrotus* (B), × 8. Note that in *Eumops* the tibia articulates with the dorsal surface of the astragalus, whereas in *Macrotus* the tibia articulates with the proximal end of the astragalus. Inset shows the posterior view of the proximal end of the calcar in *Eumops*.

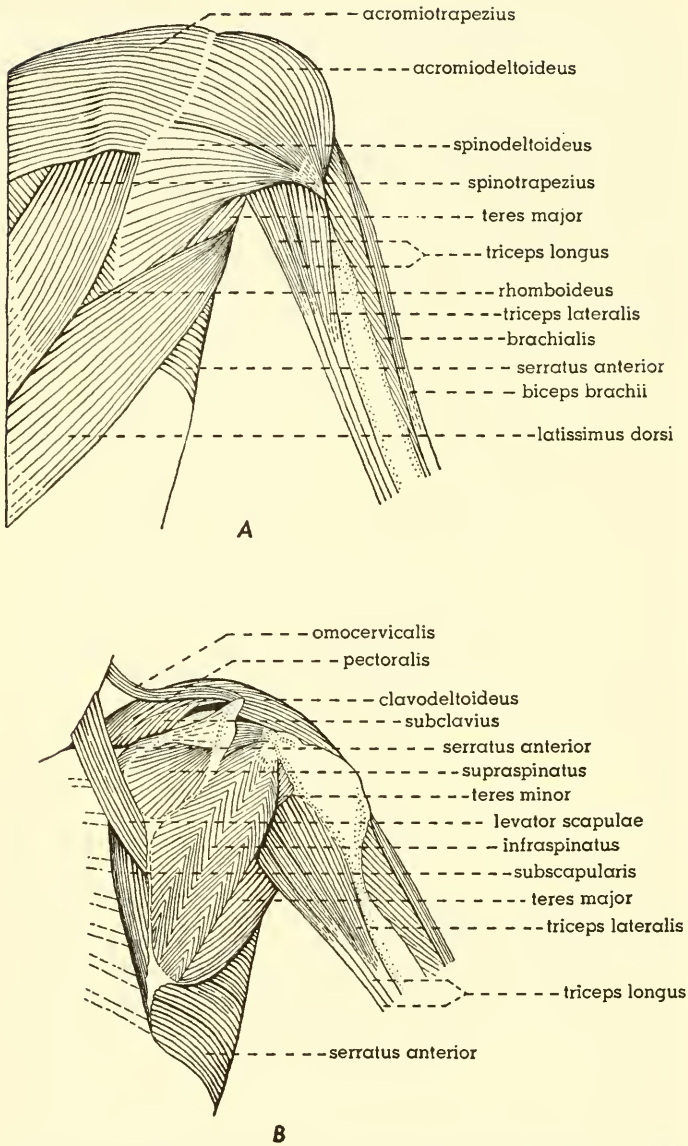

FIG. 10. A. Dorsal view of the shoulder region of *Eumops*. × 4¼. B. Dorsal view of the shoulder region of *Eumops* with some of the superficial muscles removed. × 4¼.

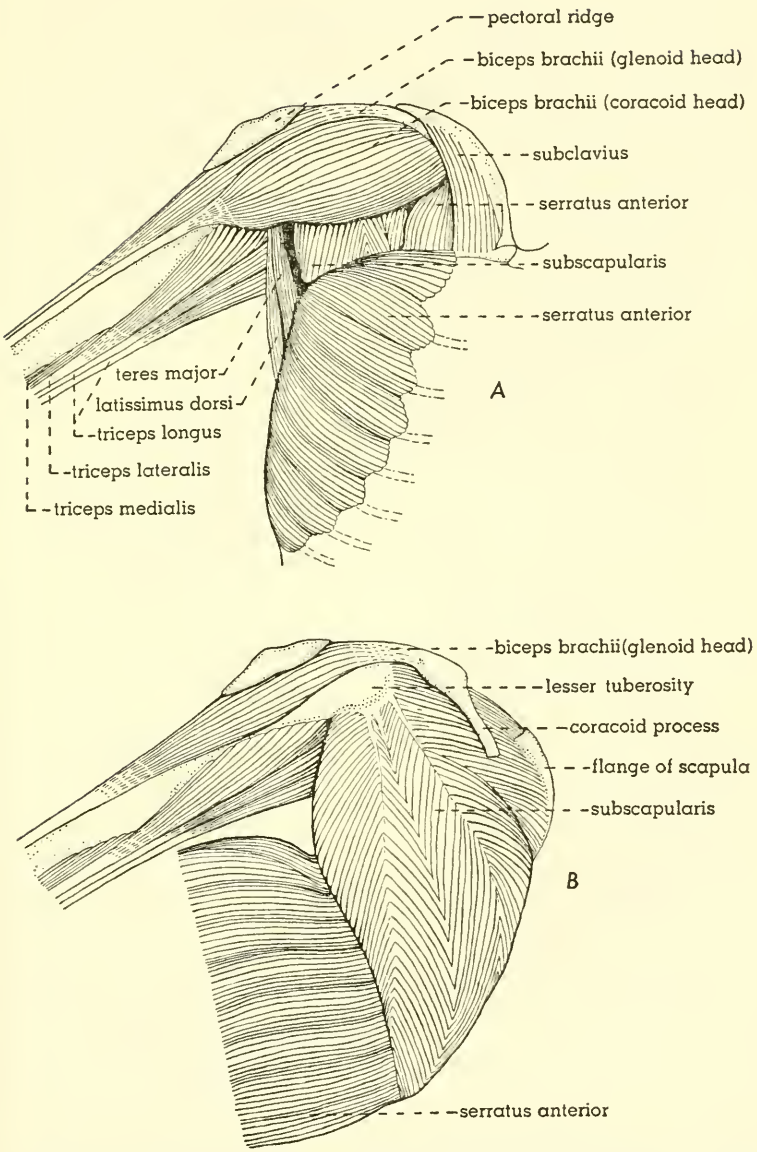

FIG. 11. A. Ventral view of the shoulder region of *Eumops*. × 4¼.
B. Ventral view of the proximal part of the forelimb of *Eumops*. × 4¼.

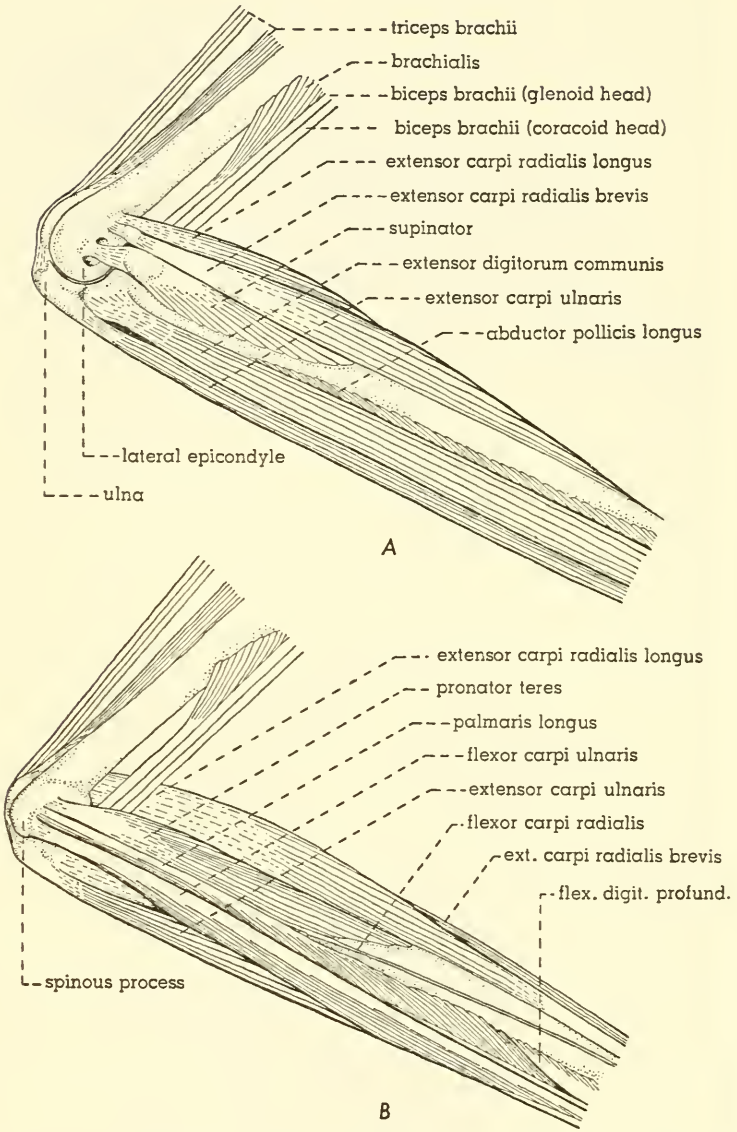

FIG. 12. A. Lateral view of the proximal part of the forearm and distal part of the upper arm of *Eumops*. × 3. B. Medial view of the same parts of the forelimb of *Eumops*. × 3.

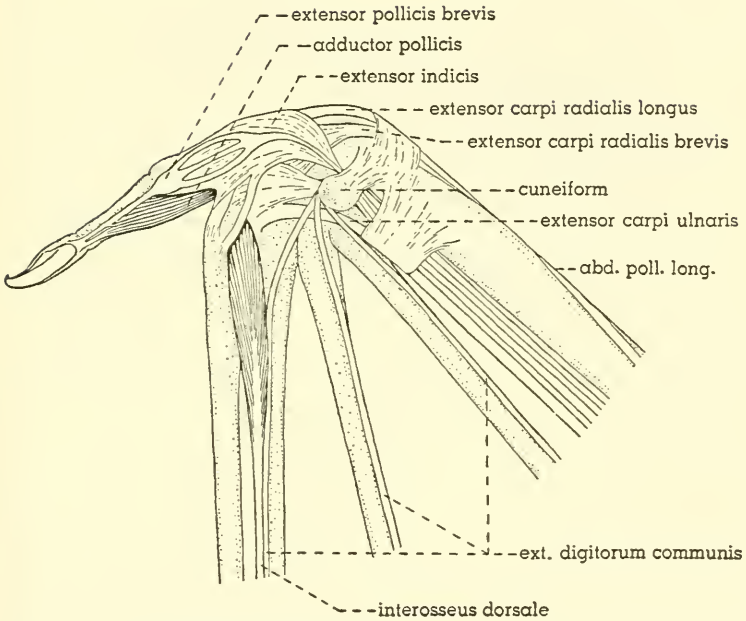

FIG. 13. Dorsal view of the wrist region of *Eumops,* showing the tendons of some extensor muscles. × 3⅓.

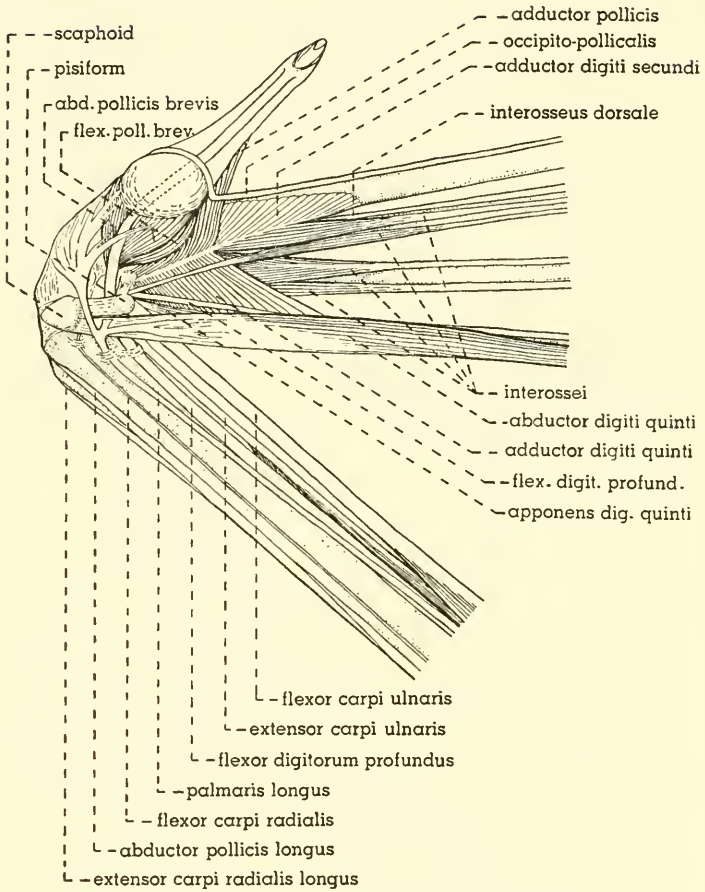

FIG. 14. Ventral view of the wrist region of *Eumops*, with part of the fascial sheet of the insertion of the M. palmaris longus removed, showing the tendons of some flexor muscles. × 3⅓.

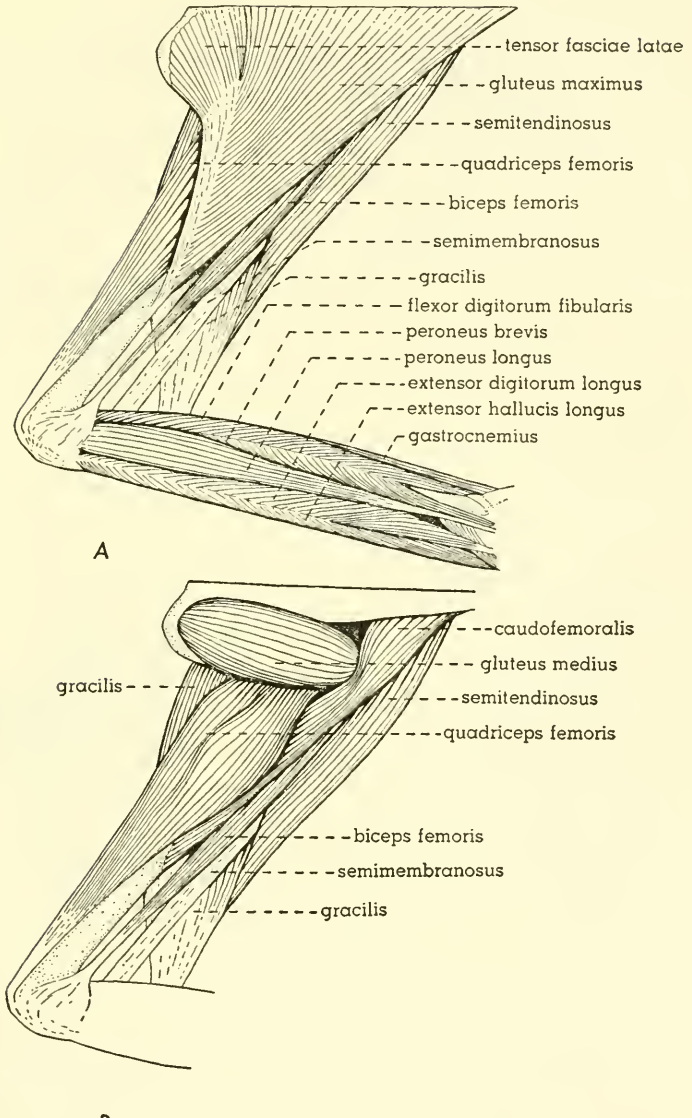

FIG. 15. A. Lateral view of the hind limb of *Eumops*. × 2⅔.
B. Lateral view of the thigh of *Eumops* with the Mm. gluteus maximus and tensor fasciae latae removed. × 2⅔

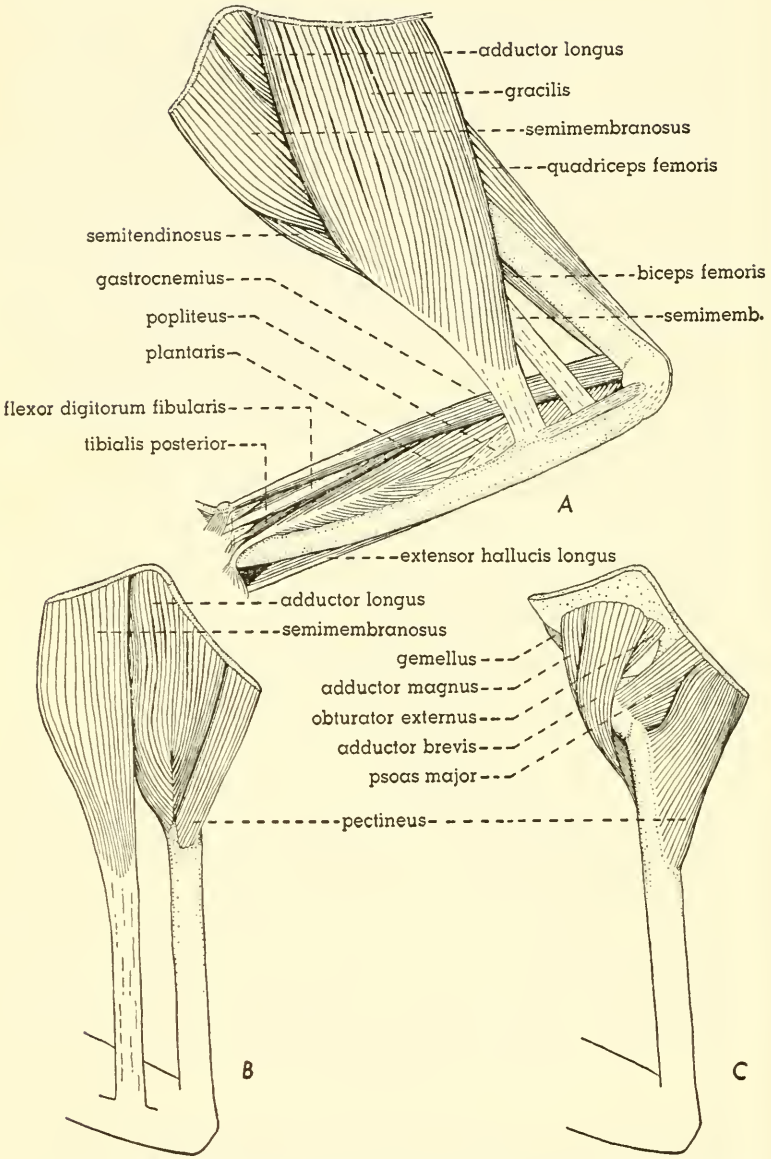

FIG. 16. A. Medial view of the hind limb of *Eumops*. × 2⅔. B and C. Progressively deeper muscles of the thigh of *Eumops* from the medial aspect. × 2⅔.

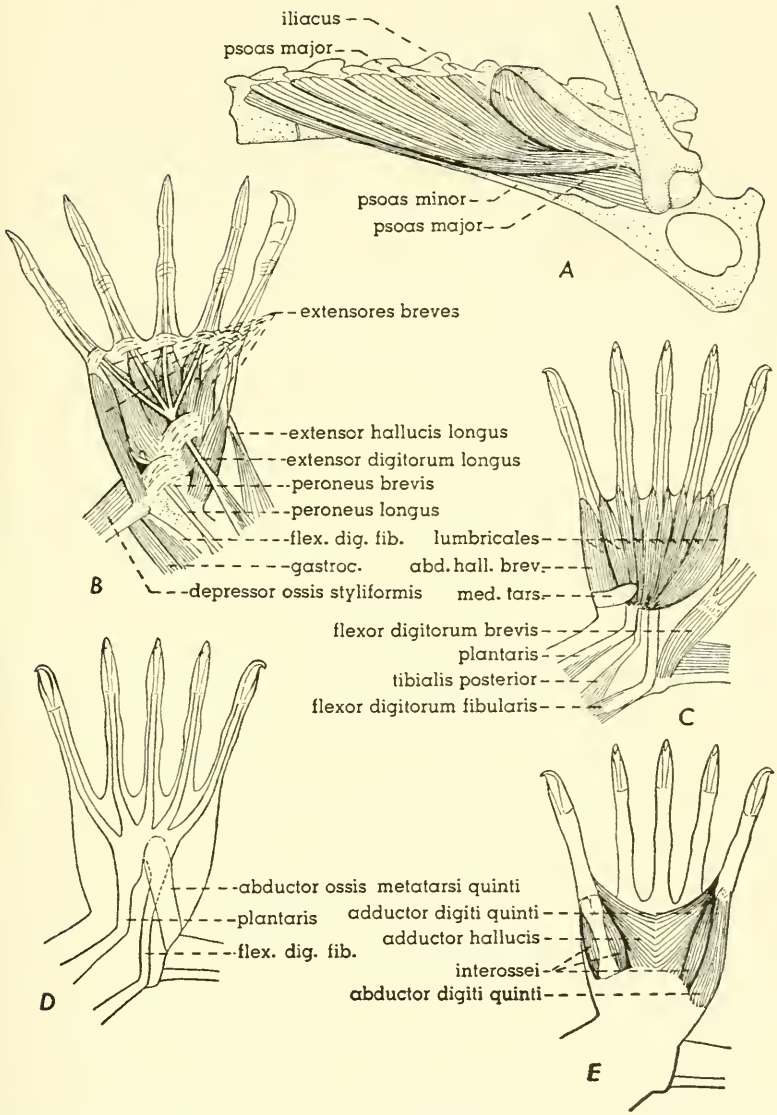

FIG. 17. A. Lateral view of the pelvic region of *Eumops*. × 5. B. Dorsal view of the left foot of *Eumops*. C, D, and E. Progressively deeper muscles of the left foot of *Eumops* from the ventral aspect. B-E are × 6⅓.

Transmitted December 23, 1958.

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15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

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2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, 10 figures in text. February 10, 1956.

4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figures in text. February 10, 1956.

5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 figure in text. March 10, 1956.

6. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. By Edwin P. Martin. Pp. 361-416, 19 figures in text. April 2, 1956.

7. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. By Henry S. Fitch. Pp. 417-476, 10 figures in text, 6 tables. June 1, 1956.

8. Food of the crow, Corvus brachyrhynchos Brehm, in south-central Kansas. By Dwight Platt. Pp. 477-498, 4 tables. June 8, 1956.

9. Ecological observations on the woodrat, Neotoma floridana. By Henry S. Fitch and Dennis G. Rainey. Pp. 499-533, 3 figures in text. June 12, 1956.

10. Eastern woodrat, Neotoma floridana: Life history and ecology. By Dennis G. Rainey. Pp. 535-646, 12 plates, 13 figures in text. August 15, 1956.

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2. Additional records and extensions of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.

5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.

6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.

7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.

8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.

9. Extensions of known ranges of Mexican bats. By Sydney Anderson, Pp. 347-351. August 15, 1956.

10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.

11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.

12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-384, 7 figures in text, 1 table. February 21, 1958.

13. A new, bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388.

14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396, 1 figure in text. December 19, 1958.

15. New subspecies of the Rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.

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3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.

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4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.

5. Birds found on the Arctic Slope of northern Alaska. By James W. Bee. Pp. 163-211, 2 plates, 1 figure in text. March 12, 1958.

6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.

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4. A new snake of the genus Geophis from Chihuahua, México. By John Legler. Pp. 327-334, 2 figures in text. January 28, 1959.

5. A new tortoise, genus Gopherus, from north-central México. By John Legler. Pp. 335-343, 2 plates. April 24, 1959.

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7. Fishes of the Big Blue river basin, Kansas. By W. L. Minckley. Pp. 401-442, 2 plates, 4 figures in text. May 8, 1959.

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Vol. 12. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 17 figures. July 8, 1959.

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The Ancestry of Modern Amphibia: A Review of the Evidence

BY

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The Ancestry of Modern Amphibia: A Review of the Evidence

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INTRODUCTION

In trying to determine the ancestral relationships of modern orders of Amphibia it is not possible to select satisfactory structural ancestors among a wealth of fossils, since very few of the known fossils could even be considered possible, and scarcely any are satisfactory, for such a selection. The nearest approach thus far to a solution of the problem in this manner has been made with reference to the Anura. Watson's paper (1940), with certain modifications made necessary by Gregory (1950), provides the paleontological evidence so far available on the origin of frogs. It shows that several features of the skeleton of frogs, such as the enlargement of the interpterygoid spaces and orbits, reduction of the more posterior dermal bones of the skull, and downward spread of the neural arches lateral to the notochord, were already apparent in the Pennsylvanian *Amphibamus* (Fig. 1), with which Gregory synonymized *Miobatrachus* and *Mazonerpeton*. But between the Pennsylvanian and the Triassic (the age of the earliest known frog, *Protobatrachus*) there was a great lapse of time, and that which passed between any conceivable Paleozoic ancestor of Urodela and the earliest satisfactory representative of this order (in the Cretaceous) was much longer still. The Apoda, so far as known, have no fossil record.

Nevertheless it should be possible, first, to survey those characters of modern Amphibia that might afford some comparison with the early fossils, and second, to discover among the known Paleozoic kinds those which are sufficiently unspecialized to permit derivation of the modern patterns. Further circumstantial evidence may be obtained by examining some features of Recent Amphibia which could not readily be compared with anything in the fossils; such are the embryonic development of the soft structures, including cartilaginous stages of the skeleton, the development and various specializations of the ear mechanism, adaptive characters associated with aquatic and terrestrial life, and so on.

COMPARISON OF MODERN ORDERS WITH THE LABYRINTHODONTS AND LEPOSPONDYLS

In both Anura and Urodela the skull is short, broad, relatively flat, with reduced pterygoids that diverge laterally from the parasphenoids leaving large interpterygoid vacuities, and with large orbits. (These statements do not apply to certain larval or perennibranchiate forms.) The skull in both orders has lost a number of primitive dermal bones in the posterior part; these are: basioccipital, supraoccipital, postparietal, intertemporal, supratemporal, and tabular. The exoccipitals form the two condyles but there are no foramina for the 11th and 12th nerves, since these are not separate in modern Amphibia. The opisthotic is missing in all

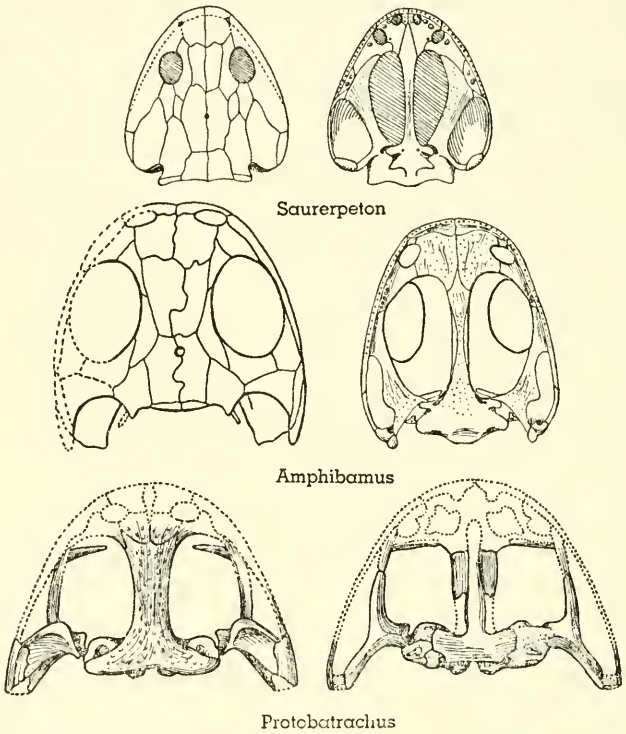

Fig. 1. *Saurerpeton* (× ½, after Romer, 1930, fig. 6); *Amphibamus*, the palatal view × 2¼, from Watson, 1940, fig. 4 (as *Miobatrachus*), the dorsal view × 2½, from Gregory's revised figure of *Amphibamus* (1950, Fig. 1); *Protobatrachus*, × 1, from Watson, 1940, fig. 18, 19.

except Proteidae (but see discussion of the ear). Although the skull is normally autostylic, a movable basipterygoid articulation is present among Hynobiid salamanders and in at least the metamorphic stages of primitive frogs, and therefore should be expected in their ancestors. The vertebrae are, of course, complete; see discussion in later section. The quadratojugal, lost in salamanders, is retained in frogs, and conversely the lacrimal, absent in frogs, occurs in a few primitive salamanders. The situation in Apoda is different, but postfrontal and jugal should be noted as bones retained in this order while lost in the others.

Thus, in spite of minor differences, the above list shows that there are numerous and detailed similarities between Anura and Urodela with respect to the features in which they differ from the Paleozoic orders. Pusey (1943) listed 26 characters which *Ascaphus* shares with salamanders but not with more advanced frogs; a few of these might be coincidental, but most of them are of some complexity and must be taken to indicate relationship. The main adaptive specializations of Anura, however, including loss of the adult tail, extreme reduction in number of vertebrae, formation of urostyle, elongation of the ilium and lengthening of the hind legs, must have appeared at a later time than the separation of that order from any possible common stem with Urodela, although they are only partially developed in the Triassic *Protobatrachus.*

Turning to the Paleozoic Amphibia, there are two groups in which some likelihood of a relationship with modern order exists. In the Pennsylvanian Trimerorhachoidea (Labyrinthodontia, order Temnospondyli) some members, such as *Eugyrinus, Saurerpeton,* and notably *Amphibamus* (Fig. 1) had short, broad heads, an expansion of palatal and orbital openings, posterior widening of the parasphenoid associated with divergence of the pterygoids, a movable basipterygoid articulation, and reduction in size (but not loss) of the more posterior dermal bones of the skull. In recognition of Watson's (1940) evidence that these animals make quite suitable structural ancestors of frogs, Romer (1945) placed *Amphibamus* in an order, Eoanura, but Gregory (1950) indicated that it might better be left with the temnospondyls. Association of the urodele stem with this group does not seem to have been proposed hitherto.

The other group of Paleozoic Amphibia that has been considered probably ancestral to any modern type is the subclass Lepospondyli, containing three orders, Aistopoda, Nectridia and Microsauria. In

these the vertebrae are complete (holospondylous), the centra presumably formed by cylindrical ossification around the notochord, and there is no evidence as to the contributions from embryonic cartilage units. It is important to note at this point that precisely the same statement can be made regarding the vertebrae of *adults* of all three Recent orders, yet for all of them, as shown in a later section, we have ample evidence of the part played by cartilage elements in vertebral development. Therefore (a) we cannot say that there were no such elements in embryonic stages of lepospondyls, and (b) it would take more than the evidence from adult vertebrae to relate a particular modern order (for example, Urodela) to the Lepospondyli. Vague similarities to Urodela have been noted by many authors in the Nectridia, Aistopoda and Microsauria, but these are not detailed and refer mainly to the vertebrae. The skulls do not show, either dorsally or in the palate, any striking resemblance to those of generalized salamanders, and certainly most known lepospondyls are too specialized to serve as the source of Urodela. It is true that the elongate bodies, small limbs, and apparent aquatic habitus of some lepospondyls accord well with our usual picture of a salamander, but such a form and way of life have appeared in many early Amphibia, including the labyrinthodonts. The family Lysorophidae (Fig. 2), usually placed among microsaurs, is sufficiently close in skull structure to the Apoda to be a possible ancestor of these, but it probably has nothing to do with Urodela, by reason of the numerous morphological specializations that were associated with its snakelike habitus.

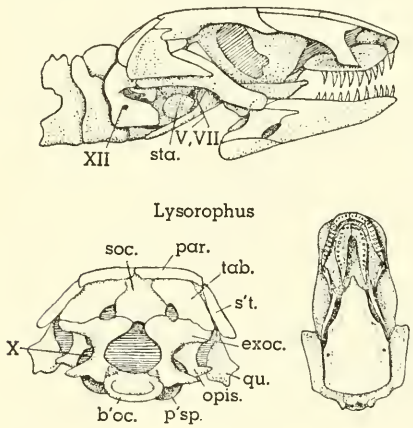

Fig. 2. *Lysorophus tricarinatus*, lateral and posterior views × 2½, modified after Sollas, 1920, Figs. 8 and 12, respectively; palatal view after Broom, 1918, × 1½. For explanation of abbreviations see Fig. 3.

McDowell's (1958) suggestion that it would be profitable to look among the Seymouriamorpha for the ancestors of frogs seems to be based upon a few details of apparent resemblance rather than a comprehensive view of the major characters of the animals. In most points which he mentions (limb girdles, form of ear, pterygoid

articulation) the present writer does not see a closer similarity of frogs to Seymouriamorpha than to Temnospondyli.

Still other opinions have been expressed. Herre (1935), for instance, concludes "on anatomical, biological and paleontological grounds" that the orders of Urodela, Anura, Apoda and Stegocephali were all independently evolved from fish, but beyond citing the opinions of a number of other authors he does not present tangible evidence for this extreme polyphyletic interpretation.

More notable are the views of several Scandinavian workers (Säve-Söderbergh, 1934; Jarvik, 1942; Holmgren, 1933, 1939, 1949a, b), of whom Jarvik, in a thorough analysis of the ethmoid region, would derive the Urodela from Porolepid Crossopterygii, and all other tetrapods from the Rhipidistia; Säve-Söderbergh and Holmgren, the latter using the structure of carpus and tarsus, see a relationship of Urodela to Dipnoi, but accept the derivation of labyrinthodonts and other tetrapods from Rhipidistia. All of this work is most detailed and laborious, and has produced a great quantity of data useful to morphologists, but the diphyletic theory is not widely adopted; the evidence adduced for it seems to consist largely of minutiae which, taken by themselves, are inconclusive, or lend themselves to other interpretation. For instance Holmgren's numerous figures of embryonic limbs of salamanders show patterns of cartilage elements that he would trace to the Dipnoan type of fin, yet it is difficult to see that the weight of evidence requires this, when the pattern does not differ in any fundamental manner from those seen in other embryonic tetrapods, and the differences that do appear may well be taken to have ontogenetic rather than phylogenetic meaning. Further, the Dipnoan specialization of dental plates and autostylic jaw suspension, already accomplished early in the Devonian, would seem to exclude Dipnoi from possible ancestry of the Urodela, an order unknown prior to the Mesozoic, in which the teeth are essentially similar to those of late Paleozoic Amphibia, and the jaw suspension is not yet in all members autostylic.

THE EAR

In temnospondylous Amphibia the tympanum generally occupied an otic notch, at a high level on the skull, bordered dorsomedially by the tabular and ventrolaterally by the squamosal. In this position the tympanum could receive airborne sounds whether the animal were entirely on land or lying nearly submerged with only the upper part of its head exposed. Among those Anura in which the ear is not reduced the same is true, except that the tabular is

lost. In Temnospondyli (Fig. 3) the posterior wall of the otic capsule was usually formed by the opisthotic, which extended up and outward as a buttress from the exoccipital to the tabular, and sometimes showed a paroccipital process for the insertion, presumably, of a slip or tendon of the anterior axial musculature. The

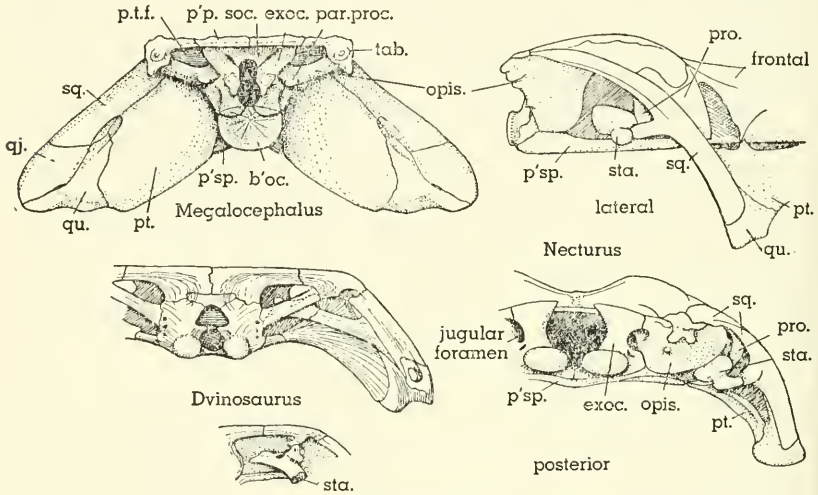

FIG. 3. Occipital region of skulls of *Megalocephalus brevicornis* (× 3/10, after Watson, 1926, as *Orthosaurus*), *Dvinosaurus* (× ¼, modified after Bystrow, 1938; the lower figure after Sushkin, 1936), and *Necturus maculosus* (× 3, original, from K. U., No. 3471).

ABBREVIATIONS USED IN FIGURES

b'd.c.—basidorsal cartilage (neural arch)
b'oc.—basioccipital
ce.$_{1-4}$—centrale$_{1-4}$
ch.—ceratohyal
clav.—clavicle
clei.—cleithrum
cor.—coracoid
d.c.$_{1-4}$—distal carpal$_{1-4}$
diap.—diapophysis
exoc.—exoccipital
ep.—episternum
hyost.—hyostapes
i.—intermedium
Mk.—Meckel's cartilage
n.—notochord
om.—omosternum
op.—operculum
opis.—opisthotic
par.—parietal
par. proc.—paroccipital process
peri. cent.—perichordal centrum
p'p.—postparietal
prep.—prepollex
pro.—prootic
p'sp.—parasphenoid
pt.—pterygoid
p.t.f.—post-temporal fossa
postzyg.—postzygapophysis
qj.—quadratojugal
qu.—quadrate
ra.—radiale
r.hy.—hyomandibular ramus of VII
rib-b.—rib-bearer
r.md.—mandibular ramus of VII
sc.—scapula
sc'cor.—scapulocoracoid
s'd.—supradorsal cartilage
s'd.(postzyg.)—supradorsal (postzygapophysis)
soc.—supraoccipital
sp.c.—spinal cord
sq.—squamosal
s'sc.—suprascapula
s't.—supratemporal
sta.—stapes
ster.—sternum
tab.—tabular
uln.—ulnare
v.a.—vertebral artery
xiph.—xiphisternum
I,IV—digits I and IV
V, VII, X, XII—foramina for cranial nerves of these numbers (in Fig. 4, VII is the facial nerve)

stapes, in addition to its foot in the fenestra ovalis and its tympanic or extrastapedial process to the tympanum, bore a dorsal process (or ligament) to the tabular, an "internal" process (or ligament) to the quadrate or an adjacent part of the squamosal, and a ligament to the ceratohyal. Some of these attachments might be reduced or absent in special cases, but they seem to have been the ones originally present both phylogenetically and embryonically in Amphibia.

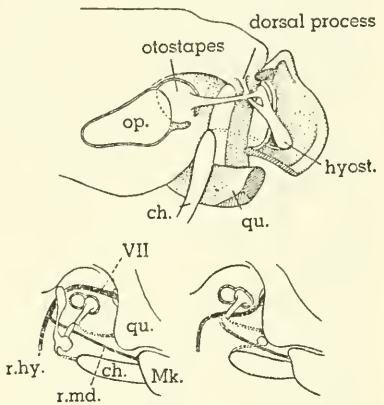

FIG. 4. Diagram of middle ear structures in *Rana* (upper figure, after Stadtmüller, 1936, and lower left after DeBeer, 1937), and *Ambystoma* (lower right, after DeBeer, 1937); all × 4. For explanation of abbreviations see Fig. 3.

Among typical frogs (Fig. 4) the base, or otostapes, is present and bony, the extrastapedial process (extracolumella, or hyostapes) is usually cartilaginous, the dorsal process (processus paroticus) is of cartilage or ligament, but the other two attachments are absent in the adult. The exoccipital extends laterally, occupying the posterior face of the otic capsule. Between it and the otostapes is a small disc, usually ossified, the operculum, which normally fits loosely in a portion of the fenestral membrane, and is developed from the otic capsule. The opercularis muscle extends from this disc to the suprascapula, in many but by no means all families of Anura.

Among Urodela (Fig. 4) the middle ear cavity and tympanum are lacking, and the stapes (columella) consists of no more than its footplate and the stylus, which is attached to the border of the squamosal, thus corresponding to the "internal" process. In families in which individuals metamorphose and become terrestrial (Hynobiidae, Ambystomidae, Salamandridae, Plethodontidae), an operculum and opercularis muscle appear in the adult, just as in frogs, except that in Plethodontidae, the most progressive family, the operculum fuses with the footplate of the stapes. Among neotenous or perennibranchiate urodeles there is no separate operculum or opercularis. The evidence given by Reed (1915) for fusion of the operculum with the columella in *Necturus* appears inconclusive, in spite of the great care with which his observations were

made. On the other hand, *Necturus* and *Proteus* alone among living salamanders have a distinct opisthotic on the posterior wall of the otic capsule (Fig. 3), as do the Cretaceous *Hylaeobatrachus* and the Eocene *Palaeoproteus*. Probably these Proteidae should be regarded as primitive in this respect, although many other features may be attributed to neoteny.

There is a contrast between Anura and most Urodela in the relative positions of the stapes and facial nerve, as shown in DeBeer's (1937) diagrams. In the latter (*Ambystoma*) the nerve is beneath, and in the former (*Rana*) above, the stapes. Judging by figures of *Neoceratodus, Hypogeophis,* and several types of reptiles and mammals, the Urodela are exceptional. *Necturus,* however, has the nerve passing above its stapes, and this may be primitive in the same sense as the persistent opisthotic. There can be, of course, no question of the nerve having worked its way through or over the obstructing stapes in order to come below it in salamanders; rather, the peripheral growth of neuron fibers in the embryo must simply pursue a slightly different course among the partially differentiated mesenchyme in the two contrasting patterns.

Although DeBeer (1937) shows in his figure of *Hypogeophis* (one of the Apoda) an operculum, this is apparently a mistake. The stapes has a large footplate, and its stylus articulates with the quadrate, but no true operculum or opercularis has been described in the Apoda. The facial nerve passes above the stapes. It does not seem necessary to regard the conditions in this order as related directly to those of either salamanders or frogs, but a reduction of the stapes comparable to that in salamanders has occurred.

The presence in both frogs and terrestrial salamanders of a special mechanism involving the opercularis muscle and an operculum cut out in identical fashion from the wall of the otic capsule behind the stapes seems to require some other explanation than that of a chance convergence or parallelism. Although the stapes and otic region are readily visible in a number of labyrinthodonts and lepospondyls, no indication of an operculum seems to be reported among them. But in the Triassic *Protobatrachus* (Fig. 1), which is unmistakably a frog in its skull, pelvis and some other features, Piveteau (1937) has shown, immediately behind the foot of the stapes, a small bony tubercle, which he and Watson (1940) designated opisthotic. Very clearly it served for insertion of a muscle, and it is equally clear that the bone is a reduced opisthotic, carrying the paroccipital process already mentioned as characteristic of it in

some temnospondyls. Since the remainder of the posterior wall of the otic capsule consists of cartilage, meeting the exoccipital, it may be that the opisthotic becomes the operculum in frogs. *Protobatrachus* was too far specialized in the Anuran direction, although it still had a tail, and the forelegs and hind legs were nearly the same size, to be considered a possible ancestor of the Urodeles. But at one stage in the general reduction of the skull in the ancestry of both groups, a condition similar to that in *Protobatrachus* may have characterized the otic region, long before the Triassic.

In the argument thus far we have considered terrestrial, adult amphibians, since it is only in these that either the normal middle ear and tympanum, or the opercular apparatus, is present. But among the urodeles several neotenic types occur (this term applies also to the perennibranchs). For most of these there is nothing about the otic region that would be inconsistent with derivation, by neoteny, from known families in which adults are terrestrial; for example, *Cryptobranchus* could have had a Hynobiid-like ancestor. But this, as mentioned above, does not hold for the Proteidae, which possess an opisthotic of relatively large size, distinctly separate from the exoccipital and prootic. Either this bone is a neomorph, which seems improbable, or there has not been in the ancestry of this particular family an episode of reduction comparable to that seen in the terrestrial families, where there is an operculum instead of a normal opisthotic. Therefore the Proteidae probably are not derived from the general stem of other salamanders, but diverged sufficiently long ago that the bones of the otic region were reduced on a different pattern. They need not be removed from the order, but, in this respect, recognized as more primitive than any other existing Urodela or Anura. A recent paper by Hecht (1957) discusses many features of *Necturus* and *Proteus*, and shows that they are remote from each other; his evidence does not seem to prove, however, that they were of independent origin or that they need be placed in separate families.

VERTEBRAE AND RIBS

Development of the vertebrae and ribs of Recent Amphibia has been studied by Gamble (1922), Naef (1929), Mookerjee (1930 a, b), Gray (1930) and Emelianov (1936), among others. MacBride (1932) and Remane (1938) provide good summaries. In this section reference will be made to the embryonic vertebral cartilages by the names used for them in these studies, although the concept

of "arcualia" is currently considered of little value in comparative anatomy.

The centrum in Anura (Fig. 5) is formed in the perichordal sheath (*Rana, Bufo*) or only in the dorsal portion thereof (*Bombinator, Xenopus*). The neural arch develops from the basidorsal cartilages that rest upon, and at first are entirely distinct from, the perichordal sheath. Ribs, present as separate cartilages associated with the 2nd, 3rd and 4th vertebrae in the larvae of *Xenopus* and

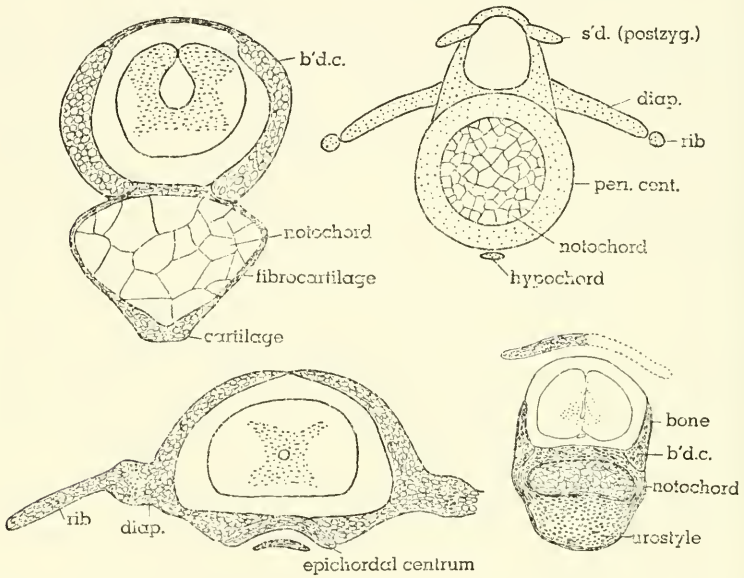

Fig. 5. Development of Anuran vertebrae. Upper left, late tadpole of *Xenopus laevis;* lower left, same just after metamorphosis; upper right, diagram of general components of primitive Anuran vertebra. (After MacBride, 1932, Figs. 35, 38, 47D, respectively.) Lower right, section through anterior portion of urostyle, immediately posterior to sacral vertebra, in transforming *Ascaphus truei* (original, from specimen collected on Olympic Peninsula, Washington). All × 20 approx. For explanation of abbreviations see Fig. 3.

Bombinator, fuse with lateral processes (diapophyses) of the neural arches at metamorphosis, but in *Leiopelma* and *Ascaphus* the ribs remain freely articulated in the adult. Basiventral arcualia have been supposed to be represented by the hypochord, a median rod of cartilage beneath the shrinking notochord in the postsacral region, which at metamorphosis ossifies to produce the bulk of the urostyle. Fig. 5, lower right, a transverse section taken immediately posterior to the sacral ribs in a transforming specimen of *Ascaphus,*

shows that the "hypochord" is a mass of cartilage formed in the perichordal sheath itself, and very obviously is derived from the ventral part of postsacral perichordal centra; there are, then, no basiventral arcualia, and the discrete hypochord shown in MacBride's diagram (Fig. 5, upper right) of a frog vertebra does not actually occur below the centrum, but only below the notochord in the postsacral region.

In Urodela (Fig. 6) the pattern of vertebral and rib development is more complex, and there has been much controversy over its

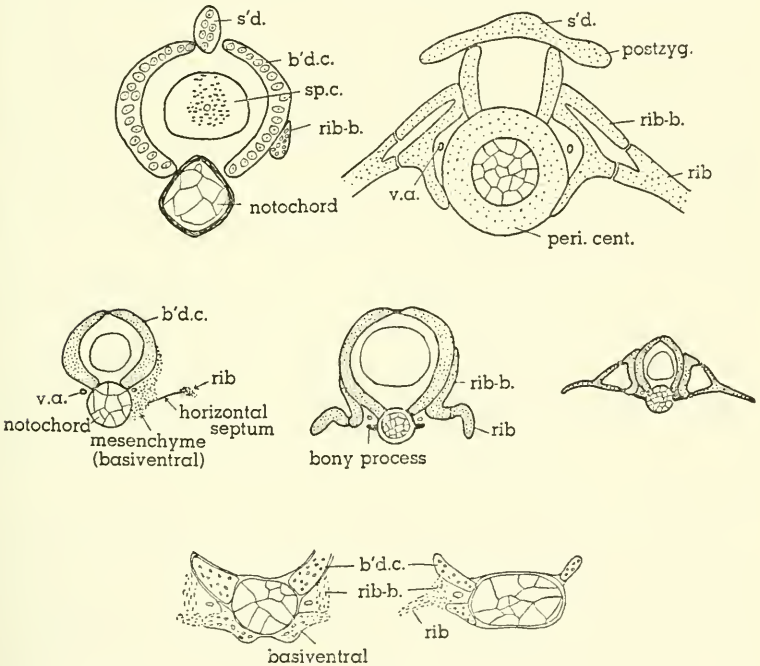

FIG. 6. Development of Urodele vertebrae. Upper figures, *Triton*: at left, larva at 20 mm., at right, diagram of components of vertebra (from MacBride, 1932, figs. 17, 47C). Middle figures, *Molge vulgaris* larva: left, at 18 mm.; middle, at 20-22 mm.; right, at 25 mm. (from Emelianov, 1936, figs. 33, 36, 38 respectively). Lower figures, *Necturus maculosus* larva: left, at 21 mm.; right, at 20 mm. (from MacBride, 1932, figs. 41.5, 41.3 respectively, after Gamble, 1922). All × 20 approx. For explanation of abbreviations see Fig. 3.

interpretation. Neural arches and perichordal centra form in the same manner as in frogs, but with the addition in certain cases (*Triton*) of a median supradorsal cartilage, which gives rise to the zygapophyses of each neural arch. Difficulty comes, however, in understanding the relationship of the ribs to the vertebrae. Each

rib, usually two-headed, articulates with a "transverse process" that in its early development seems to be separate from both the vertebra and the rib, and is therefore known, noncommittally, as "rib-bearer." This lies laterally from the centrum, neural arch, and vertebral artery; upon fusing with the vertebra it therefore encloses the artery in a foramen separate from the one between the capitulum and tuberculum of the rib (the usual location of the vertebral artery). At least four different interpretations of these structures have been suggested:

(1) Naef (1929) considered the rib-bearer a derivative of the basiventral, which, by spreading laterally and dorsally to meet the neural arch, enclosed the vertebral artery. He then supposed that by reduction of the rib-bearer in other tetrapods (frogs and amniotes) the vertebrarterial foramen and costal foramen were brought together in a single foramen transversarium. The implication is that the Urodele condition is primitive, but it cannot now be supposed that Urodela are ancestral to any other group, and the rib-bearer is most probably a specialization limited to salamanders. This does not, of course, invalidate the first part of his interpretation.

(2) Remane (1938), noting that rib insertions of early Amphibia are essentially as in Amniota, argued that the rib-bearer is not from the basiventral but is a neomorph which originates directly from the neural arch and grows ventrally. This he inferred mainly from Gamble's (1922) observation on *Necturus,* but his assumption that *Necturus* is more primitive than other salamanders (such as the Salamandridae), where the pattern differs from this, is not necessarily correct. Rather, the perennibranchs are distinguished mainly by their neotenous features, and their development is likely to show simplifications which are not necessarily primitive. The suggestion of a "neomorph" ought not to be made except as a last resort, for it is simply an acknowledgment that the author does not recognize homology with any structure already known; sometimes further information will make such recognition possible.

(3) Gray (1930), using *Molge taeniatus,* concluded that the normal capitulum of the rib was lost, but that the tuberculum bifurcated to make the two heads seen in Urodela, thus accounting for the failure of the costal foramen to coincide with that of the vertebral artery. This answer, too, seems to entail an unprovable assumption which should not be made without explicit evidence.

(4) Finally, Emelianov (1936) regarded the rib-bearer as a rudimentary *ventral* rib, on account of its relationship to the vertebral artery, and considered the actual rib to be a neomorph in the *dorsal*

position characteristic of tetrapod ribs in general. This argument would fit the ontogenetic picture satisfactorily, provided that (*a*) there were some evidence of ventral, rather than dorsal, ribs in early Amphibia, and (*b*) we accept the invention of another neomorph in modern Amphibia as an unavoidable necessity. Emelianov's conclusion (p. 258) should be quoted here (translation): "The ribs of Urodela are shown to be upper ribs, yet we find besides these in Urodela rudimentary lower ribs fused with the vertebral column. The ribs of Apoda are lower ribs. In Anura ribs fail to develop fully, but as rare exceptions rudiments of upper ribs appear."

Of these various interpretations, that of Naef seems to involve the minimum of novelty, namely, that the rib-bearer is the basiventral, expanded and external to the vertebral artery. It is not necessary to take this modification as the ancestral condition in tetrapods, of course. The basiventral (= intercentrum) would merely have expanded sufficiently to provide a diapophysis for the tuberculum as well as the (primitive) facet for the capitulum. No neomorph appears under this hypothesis, which has the distinct advantage of simplicity.

Figures of early stages in vertebral development by the authors mentioned show that the basidorsals chondrify first, as neural arches, while a separate mass of mesenchyme lies externally and ventrally from these. This mesenchyme may chondrify either in one piece (on each side) or in two; in *Molge* the part adjacent to the centrum is ossified in the 20-mm. larva, and subsequently unites with the more dorsal and lateral cartilaginous part, while the rib, appearing farther out, grows inward to meet this composite "rib-bearer." In *Necturus* the mesenchyme below the neural arch differentiates into a cartilage below the vertebral artery (position proper to a basiventral), a bridge between this and the neural arch, and a rib, the latter two chondrifying later than the "basiventral" proper. In the "axolotl" (presumably *Ambystoma tigrinum*) the rib-bearer grows downward from its first center of chondrification at the side of the neural arch (Emelianov, 1936).

Thus it appears that the simplest hypothesis to account for the rib-bearer is that (*a*) it is the basiventral, (*b*) it is recognizable just before chondrification as a mass of mesenchyme in contact with both the notochordal sheath and the basidorsal cartilage, (*c*) it may chondrify or ossify first in its ventral portion or in its dorsal portion, the two then joining before it fuses with the rest of the vertebra, (*d*) the enclosure of the vertebral artery is a con-

sequence of the extension of the basiventral beyond the position occupied by it in primitive Amphibia, and (*e*) there is no indication that this took place in other orders than the Urodela.

It seems that the vertebrae in Urodela have at least the following components: perichordal centra, separate basidorsal cartilages, and basiventrals, which are somewhat specialized in their manner of development. The vertebrae of Anura develop in the fashion just described except that basiventrals are lacking. It would seem no

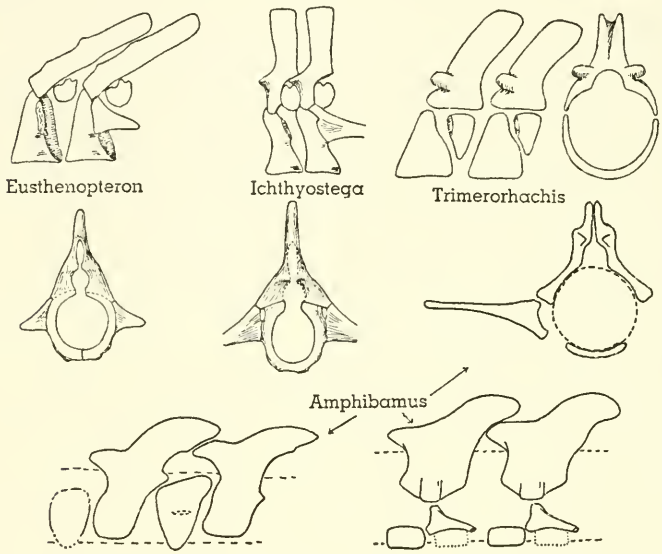

Fig. 7. Vertebrae of *Eusthenopteron* (× 1) and *Ichthyostega* (× ⅔, after Jarvik, 1952), *Trimerorhachis* (× 1½, after Case), and *Amphibamus* (× 10, after Watson, 1940) in lateral and end views; the two lower right-hand figures are from Watson (1940, as *Miobatrachus*); the lower left is from a cast of the "*Miobatrachus*" specimen in Chicago Natural History Museum, No. 2000, in the presacral region (original, × 10).

more difficult to accept the derivation of salamander vertebrae from the temnospondylous type than it is in the case of frogs, if other evidence points to such an ancestry.

Fig. 7, lower right, is Watson's (1940) illustration of the anterior trunk vertebrae of *Amphibamus* (*Miobatrachus*), in which the intercentrum is shown as a single median piece. Fig. 7, lower left, shows two of the more posterior trunk vertebrae seen as impressions in a cast of the type of "*Miobatrachus romeri;*" evidently the intercentra were paired at about the level of the 16th vertebra, and

relatively large. Gregory's (1950) figure of the type specimen of "*Mazonerpeton*" (also equivalent to *Amphibamus*) shows the anterior trunk vertebrae in relation to the ribs essentially as they appear to me in the cast of *Miobatrachus*, and rather differently from Watson's figure of the latter. Gregory is probably right in considering the specimens to represent various degrees of immaturity. So far as present information goes, then, the vertebrae of salamanders and frogs show no *clear* evidence of derivation from those of any particular group among the early Amphibia, but their features are not inconsistent with a simplification of the pattern of Temnospondyli.

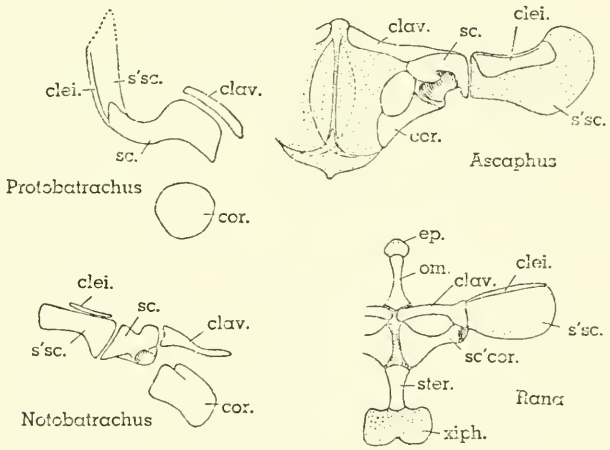

FIG. 8. Pectoral girdles of *Protobatrachus* (after Piveteau, 1937), *Notobatrachus* (after Stipanicic and Reig, 1956), *Ascaphus* (after Ritland, 1955 a) and *Rana* (original); all × 2. For explanation of abbreviations see Fig. 3.

PECTORAL GIRDLE

Hecht and Ruibal (Copeia, 1928:242) make a strong point of the nature of the pectoral girdle in *Notobatrachus*, as described recently by Stipanicic and Reig (1955, 1956) from the Jurassic of Patagonia, and quite rightly recommend that the significance of the arciferal and firmisternal types of girdle be restudied. That of *Notobatrachus* is said to be firmisternal; in view of the arciferal condition in the supposedly primitive *Leiopelma, Ascaphus, Bombinator*, etc., this comes as a surprise. Is the firmisternal girdle, as seen in *Rana, Bufo*, and others, actually the ancestral type, and has the arciferal been derived from something like this?

In the figures given by Stipanicic and Reig the ossified parts of the girdle are figured in detail (Fig. 8) and Reig's discussion of it is thorough. The decision to call it firmisternal was taken with some hesitancy, for no median elements are indicated, and the position and shape of those seen is closely similar to the ossified parts in *Ascaphus* and *Leiopelma;* there is no bony sternum or omosternum. It is safe to suppose that some cartilage lay in the midline between the clavicles and coracoids, but there is no evidence as to its extent, rigidity, or degree of overlapping if any. Apparently, then, there is not sufficient reason to infer that this Jurassic frog had a pectoral girdle comparable with the modern firmisternal type.

Piveteau (1955:261) remarks that the only living Anuran that can be compared usefully with *Protobatrachus* (Triassic) with regard to its pectoral girdle is *Ascaphus.* Again, the extent of cartilage in *Protobatrachus* (Fig. 8) can only be inferred, and there are no median elements. The agreement with *Ascaphus* includes the presence, in both, of a separate coracoid ossification situated posterior to the ossified "scapulocoracoid" (actually scapula). This ossification is evidently that shown in *Notobatrachus* as "coracoid." Direct comparison of the three genera with one another suggests that if we use the term arciferal for any, we should use it for all.

In the remote predecessor of Anura, *Amphibamus* of the Pennsylvanian, the pectoral girdle was less substantial than in many of its contemporaries, but it contained the primitive median interclavicle in addition to the clavicle, cleithrum, and scapulocoracoid. (The figure of Watson, 1940, and that by Gregory, 1950, are of individuals of different ages, the latter being older.) It is clear that the paired elements of such a girdle were held rigid by their attachment to the interclavicle, *via* the clavicles. Subsequent elimination of the interclavicle in the Anuran line of descent, and decrease of ossification, left a girdle like that of *Protobatrachus, Notobatrachus, Ascaphus* and *Leiopelma.* But in several advanced families a more rigid median "sternum," of one or two bony pieces plus cartilage, is developed secondarily, possibly (as Cope, 1889: 247, suggested) in correlation with axillary amplexus.

Among Urodela no dermal bones occur in the pectoral girdle. There is usually a scapulocoracoid ossified as a single piece, from which a thin cartilaginous suprascapula extends dorsally and a broad cartilaginous coracoid plate extends medially, overlapping the one from the opposite side; a precoracoid lobe of this reaches forward on either side, and a median, posterior "sternum" of carti-

lage may make contact with the edges of the two coracoids. In *Siren* and *Amphiuma* two centers of ossification are found for each scapulocoracoid, and in *Triton* and *Salamandra* three. Probably the more dorsal and lateral of these represents the primitive scapula and the other one (or two) the primitive coracoid.

Comparing the girdle of a salamander with that of a frog, the closest similarity can be seen between *Ascaphus* and a salamander in which the scapula and coracoid ossify separately. Both have the median "sternum" in contact with the coracoid plates. The major difference, of course, is the lack of clavicle and cleithrum in the salamander.

CARPUS AND TARSUS

In *Ascaphus* (Ritland, 1955a; cleared and stained specimens of nearly grown males) distal carpals 1, 2, 3 and 4 are present and separate, increasing in size in the order given (Fig. 9). A pre-

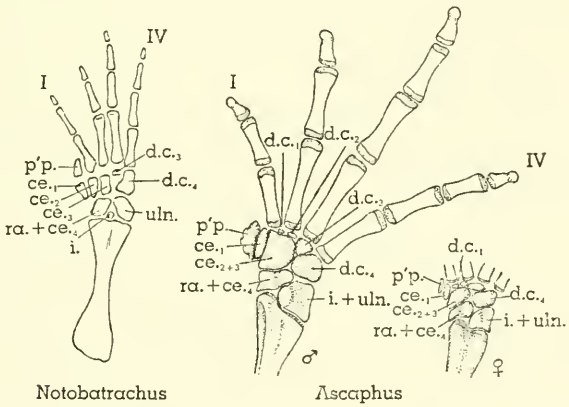

FIG. 9. Skeleton of fore foot of *Notobatrachus* (after Stipanicic and Reig, 1956, terminology revised) and *Ascaphus* (after Ritland, 1955 a); all × 5. For explanation of abbreviations see Fig. 3.

pollex rests against centrale 1; centralia 2 and 3 are fused; the radiale fuses with centrale 4, and the intermedium fuses with the ulnare; radius and ulna are fused with each other as in other frogs. The digits (and metacarpals) are considered by Ritland to be 1-4, in addition to the prepollex, rather than 2-5.

In the Jurassic *Notobatrachus* Stipanicic and Reig (1956) have shown the carpus with surprising clarity (Fig. 9). If their nomenclature of the parts be revised, we obtain a fairly close resemblance to *Ascaphus*, except that centralia 2 and 3 are not fused, distal

carpals 1 and 2 do not show (which would easily be understood if they were of the size of those in *Ascaphus*, or not ossified), and the intermedium remains separate from the ulnare.

In *Salamandra* (Francis, 1934; Nauck, 1938) distal carpals 1 and 2 are fused in both larva and adult, and 3 and 4 are separate; the radiale, intermedium and ulnare are separate in the larva but the latter two fuse in the adult; centrale 1 (labelled prepollical cartilage by Francis) and centrale 2 are separate. Francis considers the digits (and metacarpals) to be 1-4. Apparently the arrangement here indicated for the larva is characteristic of other larval salamanders, except where further reduced, and reduction below the number given for the adult is common in other terrestrial forms. The radius and ulna are, of course, separate.

The ossification of carpals is more likely to be complete in adult frogs than in salamanders, but some ossification of all parts named is found in several of the latter. A common ancester of frogs and salamanders could be expected to have the following elements present and ossified in the adult: distal carpals 1-4 separate; 3 centralia; radiale, intermedium and ulnare separate. Comparison with fossils older than *Notobatrachus* is fruitless on these points, unless we go back to forms too distant to have any special value, such as *Eryops*. This is because of inadequate preservation and because the elements are not fully ossified in many immature specimens.

For the purpose of this review there is no special value in a comparison of the tarsi of frogs and salamanders, since the leaping adaptation of the former leaves very little common pattern between them. Even in *Protobatrachus*, where the legs were not yet conspicuously lengthened, the tibiale and fibulare ("astragalus" and "calcaneum" respectively) were already considerably elongated. The carpus and tarsus of *Amphibamus* are as yet undecipherable.

THE LARVA

Considering the postembryonic developmental stages of modern Amphibia, there can be no doubt that a gill-bearing, four-legged larva of a salamander, in which lateral line pores and a gular fold are present, represents much more closely the type of larva found in labyrinthodonts than does the limbless, plant-nibbling tadpole of the Anura. Salamander-like larvae of labyrinthodonts are well known, especially those formerly supposed to comprise the order Branchiosauria. Many, perhaps the majority of, labyrinthodonts show some features associated with aquatic life even when full-

grown, as do the lepospondyls. These features may include impressions of sensory canals on the dermal bones of the skull, persistence of visceral arches, reduction in size of appendages, and failure of tarsal and carpal elements to ossify. In fact, it appears that very few of the Paleozoic Amphibia were successful in establishing themselves as terrestrial animals even as adults.

Nevertheless, in the ancestry of Anura, and that of at least the Hynobiid, Ambystomid, Salamandrid and Plethodontid salamanders, there must certainly have been a terrestrial adult, transforming from an aquatic larva. The leaping mechanism of Anura, shown in so many features of their anatomy, is perhaps to be explained as a device for sudden escape from land into the water, but it was not yet perfected in the Triassic *Protobatrachus* or the Jurassic *Notobatrachus.*

The middle ear, its sound-transmitting mechanism, and the tympanum, well developed in most Anura, are readily derived from those of early labyrinthodonts, and are presumably effective for hearing airborne sounds whether on land or while floating in the water. Reduction of these organs in Urodela may be correlated with their customary restriction to subsurface habitats and inability to maintain a floating position while in water.

Some light may be shed on the significance of the tadpole of Anura by considering the early stages of the ribbed frogs, Liopelmidae. *Leiopelma* and *Ascaphus* are so closely similar in the adult that there is no doubt that they belong in one family, primitive in some respects (including articulated ribs; pyriformis and caudalipuboischiotibialis muscles) but not in others (absence of tympanum and middle ear). In both genera the eggs are large, 5 mm. in *Leiopelma,* 4.5 mm. in *Ascaphus,* and unpigmented; but at this point the resemblance ends.

Stephenson (1955) showed that embryos of *L. hochstetteri* develop equally well on land (in damp places) or in the water, and that embryos prematurely released from egg capsules develop successfully in the water. The larvae possess both pairs of legs (Fig. 10) and a broad gular fold

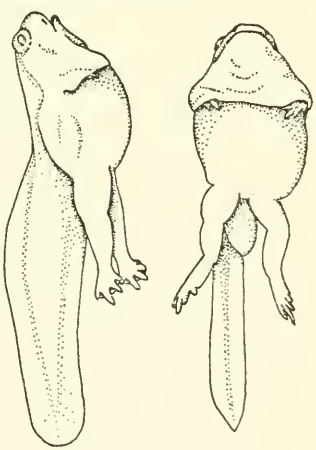

FIG. 10. *Leiopelma hochstetteri* larva, lateral and ventral (after Stephenson, 1955), × 4.

similar to that of larval salamanders. In *L. hochstetteri* the fold grows back over the forelegs temporarily, but remains free from the body and presently the legs reappear, whereas in *L. archeyi* the forelegs are not covered at any time. No branchial chamber or spiracle is formed. Of course direct development, without a tadpole, occurs in several other groups of Anura, but in each case terrestrial adaptations are obvious. This is not true of *Leiopelma,* which Stephenson regards as more nearly comparable with Urodela in its development than with other Anura, and he sees in it a "primary and amphibious" mode instead of a terrestrial specialization.

The *Ascaphus* tadpole bears no outward resemblance to the larva of *Leiopelma,* but is a normal tadpole in form, although sluggish in activity. Its greatly expanded labial folds bear numerous rows of horny epidermal "teeth," which, with the lips, serve to anchor the tadpole to stones in the swift water of mountain brooks. Noble (1927) noticed that particles of food were taken in through the external nares, and that a current of water passed through these openings and out by way of the median spiracle. It appears that any action by the teeth and jaws in scraping algae from the rocks (which were bare in the stream where I have collected *Ascaphus*) would be quite incidental, and that the lips and teeth must be primarily a clinging mechanism. Certain other mountain brook tadpoles (for example, *Borborocoetes*) show similar devices, but these are developed independently, as specializations from the usual sort of tadpole.

May it not be that closure of the gill-chamber by the opercular (= gular) fold, retardation of limb development, expansion of the lips, growth of parallel rows of horny teeth, and other correlated features that make a tadpole, were brought about as an adaptation of the primitive Anuran larva to a swift-stream habitat, and that this "basic patent" then later served to admit the tadpoles of descendant types to an alga-scraping habit in quiet water as well? The tadpole, as a unique larval type among vertebrates, bears the hallmarks of an abrupt adaptive shift, such as might have occurred within the limits of a single family, and it seems difficult to imagine the enclosed branchial chamber, the tooth-rows, and lips of a familiar tadpole as having evolved without some kind of suctorial function along the way.

SUMMARY

The Anura probably originated among temnospondylous labyrinthodonts, through a line represented approximately by *Eugyrinus, Amphibamus,* and the Triassic frog *Protobatrachus,* as shown by Watson, Piveteau and others. The known Paleozoic lepospondyls do not show clear indications of a relationship with Urodela, but *Lysorophus* may well be on the ancestral stem of the Apoda.

Between Urodela and Anura there are numerous resemblances which seem to indicate direct relationship through a common stock: (1) a similar reduction of dermal bones of the skull and expansion of palatal vacuities; (2) movable basipterygoid articulation in primitive members of both orders; (3) an operculum formed in the otic capsule, with opercularis muscle; (4) many details of cranial development, cranial muscles, and thigh muscles, especially between *Ascaphus* and the Urodela, as shown by Pusey and Noble; (5) essentially similar manner of vertebral development, quite consistent with derivation of both orders from Temnospondyli; (6) presence in the larva of *Leiopelma* of a salamanderlike gular fold, four limbs, and no suggestion of modification from a tadpole (Stephenson).

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Volume 12, No. 3, pp. 181-216, 49 figs.
February 19, 1960

The Baculum in Microtine Rodents

BY

SYDNEY ANDERSON

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The Baculum in Microtine Rodents

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The Baculum in Microtine Rodents

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SYDNEY ANDERSON

INTRODUCTION

Didier (1943, 1954) has described the bacula of several Old World microtines, and other rodents. Argyropulo studied (1933a, 1933b) five species of Cricetinae and *Microtus socialis.* Ognev (1950) illustrated numerous species of Eurasian microtines. Hamilton (1946) figured and described the baculum of 11 species of North American microtines. Hibbard and Rinker (1942, 1943) figured the baculum of *Synaptomys cooperi paludis* and of *Microtus ochrogaster taylori.* Dearden (1958) studied the baculum in two Asiatic species of *Lagurus,* in six subspecies of *Lagurus curtatus* of North America, and in six other species of microtines of other genera.

The baculum can be preserved easily with standard study skins, and is potentially useful in interpreting relationships on any taxonomic level, and especially in determining the relationships of species within a genus, if used together with other structures.

The anatomical orientation of the baculum needs comment because some confusion exists in the literature, especially concerning the use of the terms ventral and dorsal. The urethra lies on the anatomically ventral side of the penis, and of the baculum. In the center of the penis lies a single corpus cavernosum penis, shown in cross section proximal to the baculum in Figure 1c. Dorsally an artery, thinner walled than the ventral urethra, ends in a somewhat reticulate sinus surrounding primarily the middle part of the baculum within the bulbous glans penis. The corpus cavernosum penis (the structure has no median septum, at least distally) terminates with the baculum and is closely knit to it. The site of this bond is evident in the tuberosities and sculpturing of the base of the baculum.

The part of the penis enclosing the baculum, when not erect, is folded back as shown in Figures 1a and 1b. As a result the anatomically ventral surface faces upwards, or at least posterodorsally. The use of the term ventral in this account refers to the anatomically ventral side, that is to say to the side of the baculum facing the urethra.

The baculum in microtines consists of an elongate stalk, having a laterally, and to a lesser extent dorsoventrally, expanded base and

an attenuate distal shaft. Usually, three digitate processes of cartilaginous material in which additional ossifications may occur arise from the terminus of the shaft. The proportions and curvature of the stalk vary as do the proportions of the terminal ossifications to each other and to the stalk. In some species one or more of the digital processes are frequently completely unossified.

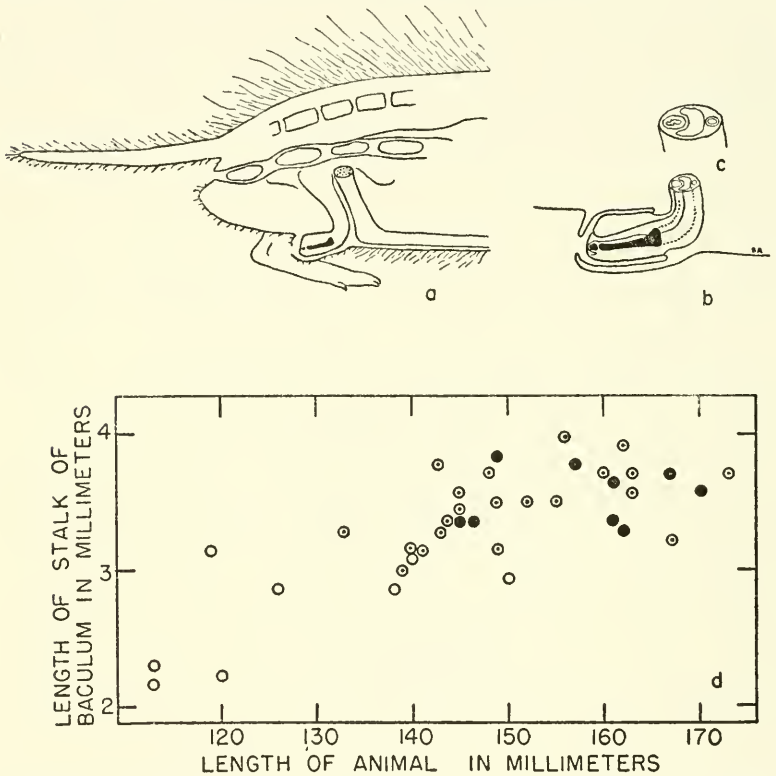


FIGURE 1. The baculum in *Microtus ochrogaster*—orientation and variation with age. *a*. Diagram of a sagittal section of the posterior half of a vole, natural size. The penis, containing the baculum (in black), extends ventrally from a point posterior to the pubic symphysis (stippled), along the body wall, and bends posteriorly at the distal end. *b*. Distal end of penis (×2) showing baculum (in black), the urethra (solid lines) adjacent to the baculum, and the corpus cavernosum (broken lines) proximal to the baculum. *c*. Oblique view of the cross section of penis (×4) shown in Figure 1 *b*. The thick-walled urethra lies ventral to the curved corpus cavernosum. A thinner-walled blood-vessel lies dorsal to the corpus cavernosum. The anatomically ventral side of the baculum, in the normal non-erect penis shown, is seen to face dorsally. *d*. Graph showing the relationship between size of baculum, size of animal, and development of digital ossifications. Circles show presence of ossification in stalk only; circles enclosing dots indicate presence of secondary ossification in median process also; large dots indicate the addition of tertiary ossification in one or both of the lateral digitate processes.

Preserved specimens of *Microtus arvalis, Microtus agrestis, Microtus orcadensis, Microtus nivalis, Microtus guentheri, Microtus subterraneus, Clethrionomys glareolus,* and *Ellobius lutescens* were provided by Prof. Robert Matthey of Lausanne, Switzerland. J. Knox Jones, Jr. carefully saved the bacula with specimens of *Microtus fortis* and *Clethrionomys rufocanus* from Korea. Dr. W. B. Quay, Department of Zoology, University of California, supplied specimens of *Synaptomys cooperi, Phenacomys intermedius,* and *Microtus oregoni.* Dr. Franklin Sturges and Mr. John W. Goertz, Museum of Natural History, Oregon State College, Corvallis, have provided specimens including bacula of *Clethrionomys occidentalis, Microtus oregoni,* and *Microtus townsendii.* Dr. Randolph L. Peterson and Mr. Bristol Foster, Royal Ontario Museum of Zoology, Toronto, Canada, provided specimens of *Phenacomys intermedius.* Dr. J. N. Layne, University of Florida, Gainsville, Florida, presented me with a baculum of *Microtus parvulus.*

I am indebted to all of these persons for their aid, and to various collectors for the Museum of Natural History, who preserved bacula with specimens. Many of these specimens were obtained through the assistance of the University of Kansas Endowment Association and the National Science Foundation.

METHODS

Bacula were obtained from fresh specimens, specimens preserved in alcohol or formalin, and dried study skins. The processing of bacula has been discussed by Hamilton (1946), Friley (1947), White (1951), and Dearden (1958). The methods used to preserve bacula for my study differed some from any of those reported. The terminal part of each penis including the baculum imbedded in the glans penis was removed in its entirety and placed in a vial. The catalogue number was kept with each specimen at all times. A two per cent solution of potassium hydroxide was added. All specimens were examined at least once a day. If tissues other than the glans penis were present they were removed with forceps when softened usually at the end of one day. Several drops of Alizarin red-S stain in a saturated alcoholic solution were added to the 3 to 5 ccs. of KOH solution in each vial. Solutions were replaced if they became turbid enough to obstruct observation of the clearing penis. After one day the solution containing stain was removed and replaced with two per cent KOH solution without stain. When the glans became sufficiently cleared that the stained baculum could be seen easily, the solution was replaced by glycerin in which clearing was completed. The time required for the entire process varied from one day to more than two weeks depending on the size of the specimen and on its condition. Fresh specimens clear more rapidly than dried specimens, and those that are dried more rapidly than those that are preserved. A three or four per cent solution of hydroxide will hasten the process, but more frequent observation is required to prevent excessive maceration.

Specimens were then examined in a shallow dish containing glycerin under a binocular microscope. The baculum can be viewed from any desired direction. The method described above leaves the baculum intact within the glans penis; therefore its orientation can be determined relative to the thick walled urethra and the thin walled dorsal artery that extends onto the dorsal side of the baculum. The ventral curvature of the penis proximal to the baculum, and the distal extension, characteristic of most species, of the dorsal border of

the glans (both shown in Figure 1) are other features aiding in correctly orienting cleared specimens. The digitate processes are not so often injured, lost, or displaced when the method described above is used as they are when the penis is dissected. Specimens were stored in glycerin in glass shell vials having polyethylene stoppers. A small card bearing the name, number, locality, and other data was placed in each vial. A specimen thus enclosed can be kept indefinitely, or removed and mounted in balsam as described by White (1951:631) or in plastic as described by Dearden (1958:541) and thus stored in the vial containing the skull of the specimen.

Drawings were made on millimeter ruled paper while the baculum was viewed under a binocular microscope with a square ruled eyepiece.

Unless otherwise noted all specimens listed are in the University of Kansas Museum of Natural History. Catalogue numbers are cited. Measurements are accurate to within less than one-tenth of a millimeter. Proportions as stated in the text are approximations, accurate to within one-twelfth (8.33 per cent). The range of variation is unknown for some species. Mention is made if maturity is known or suspected to differ in specimens being compared.

The development of the baculum has been studied by Callery (1951) in *Mesocricetus auratus* and by Ruth (1934) in the laboratory rat. In the rat (*Rattus norvegicus*) the bone is of endoblastemal origin being laid down by a condensation of undifferentiated mesenchymal cells. At the distal end of the bone dense fibrous tissue is then differentiated and at the proximal end hyaline cartilage. Growth is by substitution at the proximal end and by subperiosteal lamellation circumferentially. A marrow cavity is formed by resorption. In the baculum of the hamster the primary center of ossification is in the stalk, and is present at the age of three days; the secondary centers are in lateral processes and are present at 80 days and enlarge subsequently. A tertiary center, in each median process, may or may not develop later. Maximum development of the baculum is reached late in the reproductive life of the hamster.

The early ossification of the baculum noted in the rat and the hamster occurs in *Microtus* also. A specimen of *Microtus montanus fusus* (76831, from 5 mi. N, 26 mi. W Saguache, 9600 ft., Saguache County, Colorado) only 74 mm. in total length and weighing only 6.6 grams, had a slender ossified baculum having enlarged ends. This vole was one-half of the average length and less than one-fifth of the average weight of an adult, and of approximately the size at which weaning takes place.

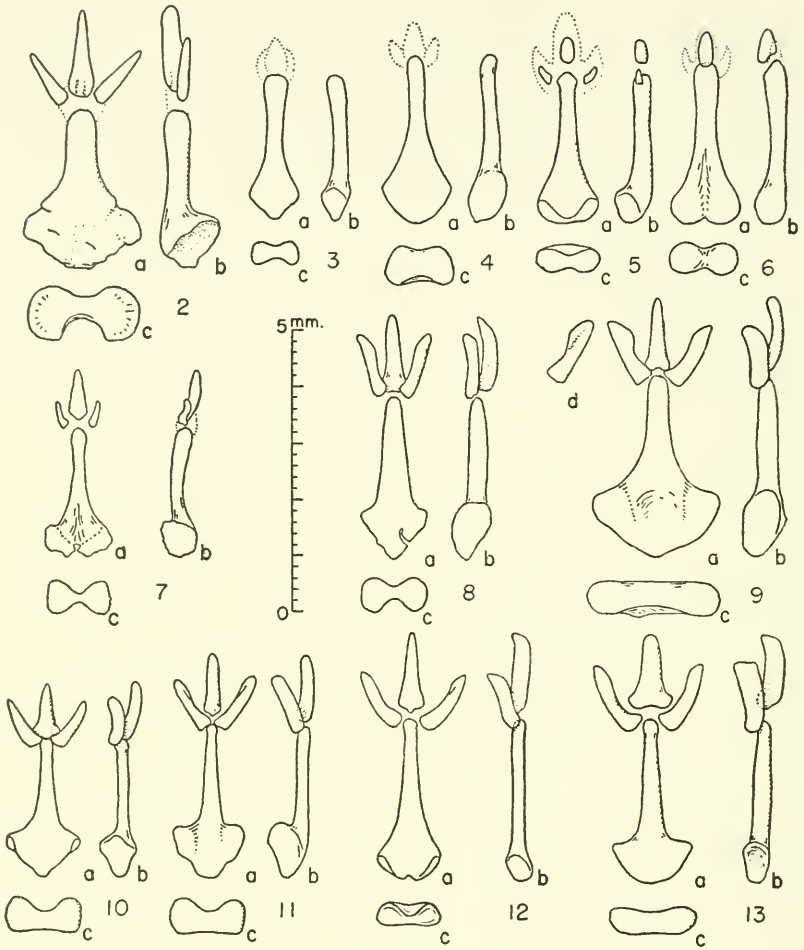
The development of the baculum in *Microtus ochrogaster* was studied in 32 specimens of various ages. The specimens (between Nos. 74994 and 75074) were collected between August 15 and September 4, 1957, at localities on the Great Plains. These specimens were from breeding populations, as evidenced by pregnancy of females and by large size of testes of males. The length and width of the stalk of the baculum, the presence of digital ossifications, the

total length of the animal, and the size of the testes were noted. Variability in length of testes is greatest when voles are from 140 to 150 mm. in total length. Sexual maturity is reached rather abruptly when the total length of most individuals is 140 to 150 millimeters. If the baculum likewise underwent more rapid growth at the onset of sexual maturity, greater variability should be evident in the length of the baculum of voles 140 to 150 mm. in total length than in bacula of voles of other sizes. This was the case (see Figure 1d). The baculum does not, however, suddenly reach its maximum maturity.

The primary ossification is in the stalk. The secondary ossification is in the median process except in *Lagurus* (Dearden, 1958:551) and some individuals of *Neofiber* (see account on page 258). Tertiary centers of ossification are in the lateral processes. The primary ossification is present at an early age and subsequently increases in size and solidity. The secondary and tertiary ossifications are progressively more common in older voles. The increase in degree of ossification of all parts continues after sexual maturity is reached. Individual variation and variation with age in the baculum of *Microtus pennsylvanicus* have been illustrated by Hamilton (1946:380). Figures 14, 15, and 17 illustrate variation with size, which is correlated with age, and also illustrate individual variation. The three bacula are from adult voles having testes that measured 15, 16 and 16 mm. in length, respectively. Each vole was trapped in late June. The total lengths in millimeters of the three voles are 172, 167, and 181; weights are 55, 52.4, and 65.5 grams. I judge that the greater size of the stalk and the better developed base shown in Figure 17 than in Figure 15 are illustrative of age variation; the difference in the size of the lateral digitate processes is, in this case, attributable to individual variation. Differences in the distal end of the baculum in Figures 42 and 43, show individual variation also. Figures 35 and 36 represent two different subspecies; different individuals of *M. mexicanus mogollonensis*, however, exhibit individual variation of the same degree.

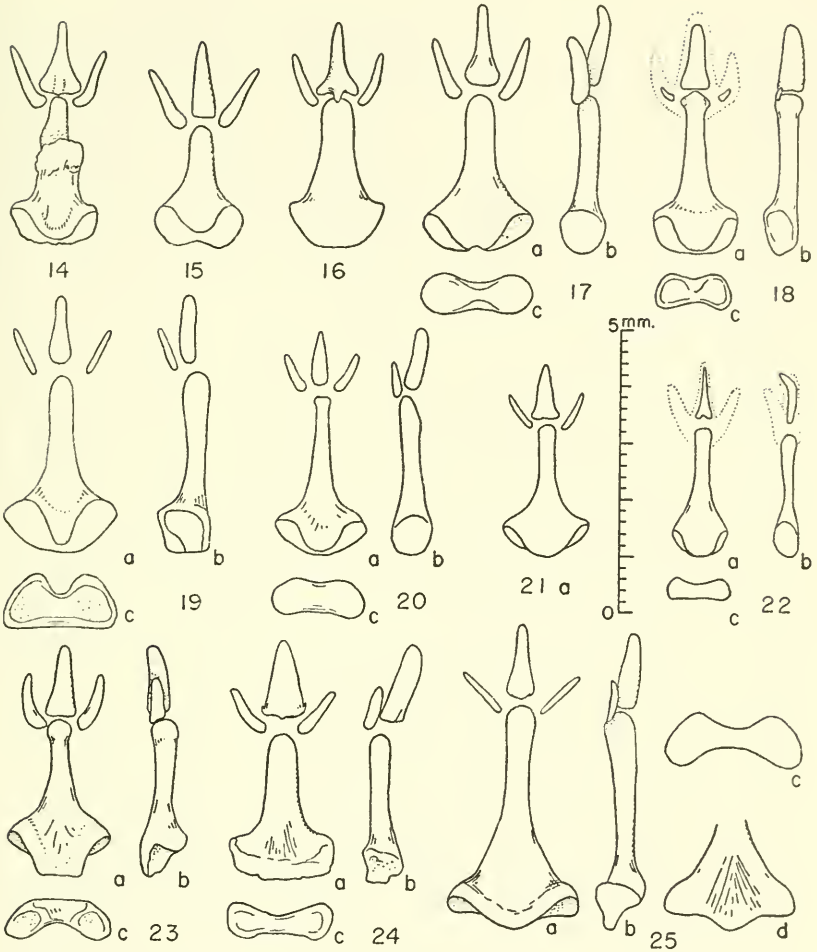
Hall and Cockrum (1953) list 44 species of microtines in North America. At least twelve of these are insular or local forms perhaps derived from some other species; for example *Microtus coronarius*, an insular form derived from *Microtus longicaudus; Microtus provectus*, considered by Chamberlain (1954:587) and by Wheeler (1956:176) as a subspecies of *Microtus pennsylvanicus;* and *Microtus ludovicianus*, a close relative of *Microtus ochrogaster.*

All North American genera have been studied. Of the genus *Microtus* in North America, all subgenera but *Orthriomys* and all species but the following nine, have been studied: *M. (Orthriomys) umbrosus*, the insular *M. (Stenocranius) abbreviatus, M. (Microtus) breweri, M. (Microtus) nesophilus, M.*



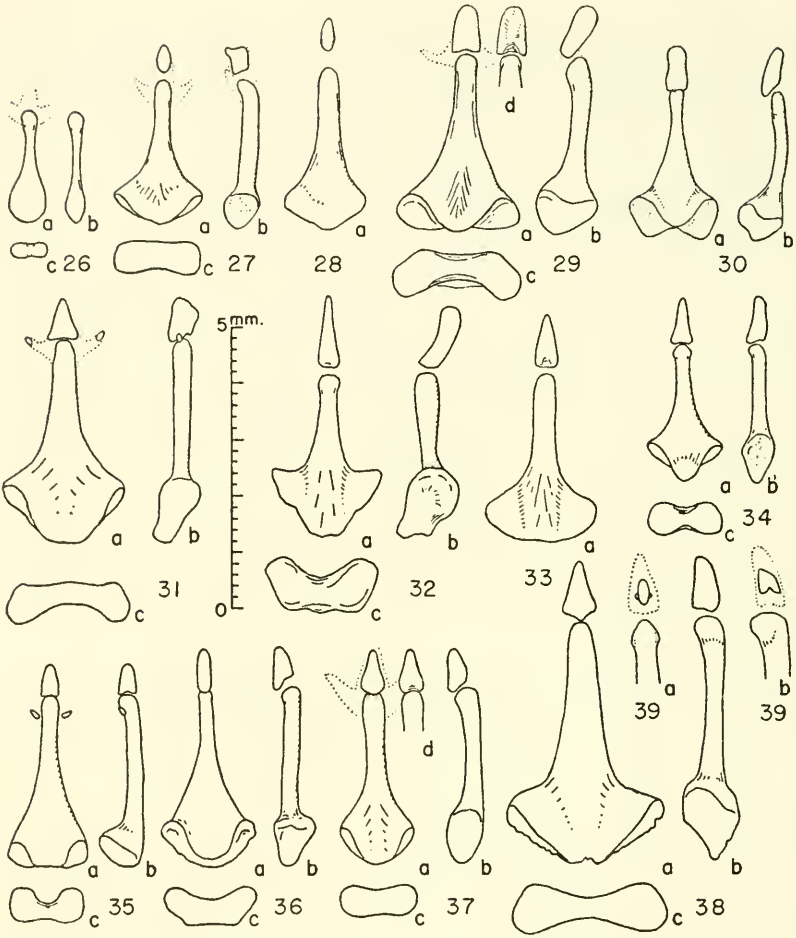
FIGURES 2-13. Bacula of microtines. Unless indicated otherwise views are (*a*) of the dorsum, (*b*) the right side, and (*c*) the proximal end with the dorsal surface upward. Exact localities are given in accounts of species concerned.

2. *Lemmus trimucronatus,* 50678, Point Barrow, Alaska.
3. *Dicrostonyx groenlandicus,* 50539, Porcupine Lake, Brooks Range, Alaska.
4. *Dicrostonyx groenlandicus,* 52524, Point Barrow, Alaska.
5. *Synaptomys cooperi saturatus,* WBQ 3-C-454, 3 mi. S Demotte, Indiana.
6. *Synaptomys cooperi paludis,* 13716, Meade County State Park, Kansas.
7. *Phenacomys intermedius celatus,* SA 2044, Quebec.
8. *Phenacomys intermedius intermedius,* WBQ 3-C-309, 5.4 mi. S Moran, Teton Co., Wyoming.
9. *Clethrionomys rufocanus,* 60438, 1 mi. NW Oho-ri, Korea, (*d*) ventral view.
10. *Clethrionomys gapperi,* 42108, 31 mi. N Pinedale, Wyoming.
11. *Clethrionomys rutilus,* 42865, 5 mi. NNE Gulkana, Alaska.
12. *Clethrionomys occidentalis,* FWS 30, Mary's Peak, Benton Co., Oregon.
13. *Clethrionomys glareolus,* 67100, Zermatt, Valais, Switzerland.



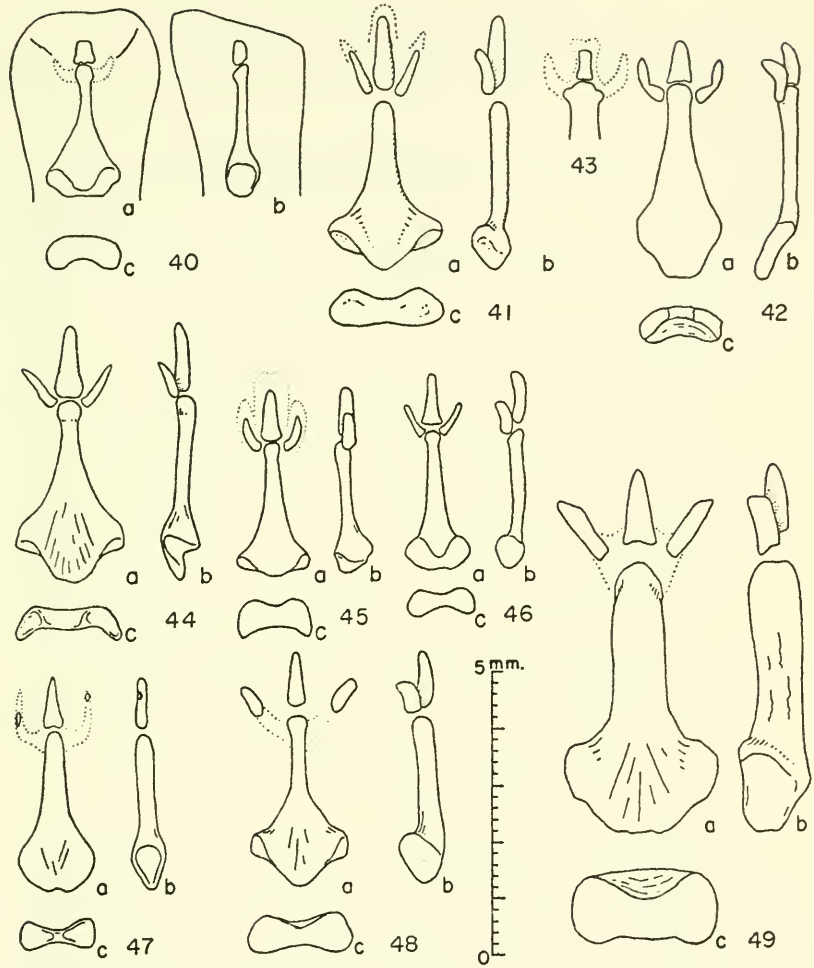
FIGURES 14-25. Bacula of *Microtus*. Unless indicated otherwise views are (*a*) of the dorsum, (*b*) the right side, and (*c*) the proximal end with dorsal surface upward.

14. *M. pennsylvanicus*, 42439, 1 mi. S, 2 mi. E Eagle Nest, Colfax Co., New Mexico; abnormality perhaps owing to injury; dorsal view.
15. *M. pennsylvanicus*, 42306, 5 mi. N, 26 mi. W Saguache, Colorado; dorsal view.
16. *M. pennsylvanicus*, 43043, 20 mi. NE Anchorage, Alaska, ventral view.
17. *M. pennsylvanicus*, 42430, 1 mi. S, 2 mi. E Eagle Nest, New Mexico.
18. *M. agrestis*, 67102, Gryon, Switzerland.
19. *M. montanus amosus*, 62241, ½ mi. E Soldier Summit, Wasatch Co., Utah.
20. *M. montanus nanus*, 57470, 2 mi. N, 2 mi. W Pocatello, Idaho.
21. *M. montanus fusus*, 42307, 5 mi. N, 26 mi. W Saguache, Colorado.
22. *M. arvalis*, 67101, Vidy, Switzerland, possibly not mature.
23. *M. guentheri*, 67104, Palestine.
24. *M. orcadensis*, 67106, Orkney Islands, orientation uncertain.
25. *M. fortis*, 63841, Chipo-ri, Korea, (*d*) ventral view.



FIGURES 26-39. Bacula of microtines. Unless indicated otherwise views are (*a*) of the dorsum, (*b*) the right side, and (*c*) the proximal end with the dorsal surface upward.

26. *M.* (*Pitymys*) *fatioi*, 67103, Zermatt, Switzerland, immature.
27. *M.* (*Pitymys*) *pinetorum*, 76834, 2 mi. N Baldwin, Douglas Co., Kansas.
28. *M.* (*Pitymys*) *pinetorum*, 68545, 1 mi. NE Pleasant Grove, Kansas.
29. *M.* (*Pitymys*) *quasiator*, 30709, Teocelo, Veracruz, (*d*) ventral view.
30. *M.* (*Pitymys*) *quasiator*, 19878, 5 km. N Jalapa, Veracruz.
31. *M.* (*Pedomys*) *ochrogaster*, 75036, 1 mi. N, 2 mi. E Oberlin, Kansas.
32. *M.* (*Stenocranius*) *miurus*, 51152, Lake Schrader, Brooks Range, Alaska.
33. *M.* (*Stenocranius*) *miurus*, 51169, Lake Schrader, Brooks Range, Alaska.
34. *M.* (*Stenocranius*) *gregalis*, 8059, "Eastern Europe."
35. *M. mexicanus mexicanus*, 63094, Valle de Bravo, Estado de México, México.
36. *M. mexicanus mogollonensis*, 63298, Mt. Taylor, Valencia Co., New Mexico.
37. *M. californicus*, 76828, 1 mi. NE Berkeley, California; (*d*) ventral view.
38. *M.* (*Arvicola*) *richardsoni*, 42454, 31 mi. N Pinedale, Sublette Co., Wyoming.
39. *M. richardsoni*, 37903, 23½ mi. S, 5 mi. W Lander, Wyoming; distal end.



FIGURES 40-49. Bacula of microtines. Unless indicated otherwise views are (*a*) of the dorsum, (*b*) the right side, and (*c*) the proximal end with the dorsal surface upward.

40. *Microtus* (*Pitymys*) *parvulus*, UF 1508, 1 mi. W Micanopy, Florida.
41. *Microtus townsendii*, 79186, Sec. 33, T. 11S, R. 5W, Benton Co., Oregon.
42. *Microtus* (*Herpetomys*) *guatemalensis*, 65895, 2 mi. S San Juan Ixcoy, Guatemala.
43. *M. guatemalensis*, 65921, 10 mi. E, 4 mi. S Totonicapan, Guatemala, dorsal view of tip.
44. *Microtus oeconomus*, 43048, Kelsall Lake, British Columbia.
45. *Microtus* (*Chilotus*) *oregoni*, WBQ 3-C-248, 5 mi. N Orick, California.
46. *Lagurus* (*Lemmiscus*) *curtatus*, 26053, 9 mi. S Robertson, Uinta Co., Wyoming.
47. *Microtus* (*Chionomys*) *nivalis*, 65127, Wetterstein, Germany, orientation uncertain.
48. *Microtus* (*Chionomys*) *longicaudus*, 50253, Crane Flat, Mariposa Co., California.
49. *Neofiber alleni*, 27268, 2 mi. S Gainesville, Florida, orientation uncertain.

(*Microtus*) *provectus* (the last three are probably insular derivatives of *M. pennsylvanicus*), *M.* (*Microtus*) *fulviventer* (perhaps derived from the same stock as *Microtus mexicanus*), *M.* (*Microtus*) *xanthognathus* (perhaps related to *Microtus chrotorrhinus*), *M.* (*Microtus*) *coronarius*, and *M.* (*Pedomys*) *ludovicianus*.

SPECIES OF WHICH BACULA WERE EXAMINED

Subfamily: Microtinae	Number of Specimens
Tribe: Lemmi	
Dicrostonyx groenlandicus (Traill)	4
Lemmus trimucronatus (Richardson)	6
Synaptomys cooperi Baird	5
Tribe: Microti	
Genus: *Clethrionomys* Tilesius, 1850	
Clethrionomys rutilus Pallas	4
Clethrionomys gapperi (Vigors)	9
Clethrionomys occidentalis (Merriam)	1
Clethrionomys glareolus Schreber	1
Clethrionomys rufocanus Sundevall	1
Genus: *Phenacomys* Merriam, 1897	
Phenacomys intermedius Merriam	5
Genus: *Ondatra* Link, 1795	
Ondatra zibethicus (Linnaeus)	1
Genus: *Microtus* Schrank, 1798	
(Herpetomys) guatemalensis Merriam	3
(Arvicola) richardsoni (DeKay)	2
(Chilotus) oregoni (Bachman)	3
(Stenocranius) gregalis (Pallas)	1
(Stenocranius) miurus Osgood	9
(Chionomys) longicaudus (Merriam)	6
(Chionomys) nivalis Martins	2
(Microtus) arvalis (Pallas)	1
(Microtus) orcadensis Millais	1
(Microtus) guentheri Danford and Alston	1
(Microtus) fortis Büchner	2
(Microtus) montanus (Peale)	15
(Microtus) townsendii (Bachman)	3
(Microtus) oeconomus (Pallas)	10
(Microtus) mexicanus (Saussure)	13
(Microtus) californicus (Peale)	2
(Microtus) pennsylvanicus (Ord)	13
(Microtus) agrestis (Linnaeus)	1
(Pedomys) ochrogaster (Wagner)	41
(Pitymys) pinetorum (LeConte)	2
(Pitymys) parvulus (Howell)	1
(Pitymys) quasiater (Coues)	5
(Pitymys) fatioi Mottaz	1
Genus: *Neofiber* True, 1884	
Neofiber alleni True	2
Genus: *Lagurus* Gloger, 1841	
Lagurus curtatus (Cope)	7
Total number examined	184

ACCOUNTS OF SPECIES

Dicrostonyx groenlandicus (Traill)

Figs. 3 and 4

Baculum: stalk elongate, greatest length (3.1 mm.) 2⅕ to 2½ times greatest breadth, and 4½ times greatest depth; digitate processes usually cartilaginous, occasionally lateral processes partly ossified; basal tuberosities weakly to moderately developed, medially confluent; posterior profile in dorsal view rounded with rounded posterior apex or shallow notch; dorsal concavity in end-view shallower and not so wide as ventral concavity; median constriction approximately ⅔ greatest depth; ventral part of base in end-view wider than dorsal part; shaft straight or slightly curved; base of stalk placed dorsally relative to axis of shaft; stalk spatulate, sometimes with distal enlargement; at mid-point stalk wider than high; lateral profile in dorsal view sloping gradually without abrupt curvature anterior to point of greatest width.

The baculum of *Dicrostonyx torquatus* figured by Ognev (1948:476) agrees with that of *D. groenlandicus* in shape of stalk, and in lateral digitate processes that are small relative to size of median process; but differs in more elongate, terminally enlarged, bulbar shape of median process. None of my specimens showed ossification in the lateral processes, observed by Hamilton (1946:381) in *Dicrostonyx rubricatus richardsoni* [= *D. groenlandicus richardsoni*]. In all of my specimens the cartilaginous median process was larger than that figured by Hamilton, or by Dearden (1958:542).

Specimens examined: Four from; Point Barrow, Alaska, 52524 (Barrow Village), 67264 (died in captivity); Brooks Range, Alaska, 50536 (Wahoo Lake, 69°08′, 146°58′), 50539 (Porcupine Lake, 68°51′57″, 146°29′50″, 3140 ft.).

Lemmus trimucronatus (Richardson)

Fig. 2

Baculum: Stalk heavy, broad, greatest length (2.8 mm.) in mature individuals (Fig. 2) as little as 1⅓ times greatest breadth, greatest length no less than 2⅔ times greatest depth of base; three ossified processes, median one from as long as to ½ longer than the lateral processes, and approximately ⅔ wider and twice as deep as lateral processes; length of median process almost 3½ times its breadth, approximately ½ length of stalk; basal fossae broadly confluent; posterior profile in dorsal view evenly rounded; in end-view ventral concavity deeper than dorsal concavity, constriction as little as ½ greatest depth in mature specimens; shaft straight, bluntly rounded, or slightly decurved and laterally inflated terminally; lateral profile in dorsal view a gradual slope from widest point of stalk anteriorly onto shaft; in younger individuals stalk slenderer, otherwise as described above.

Five specimens examined by me differ from one figured and described by Hamilton (1946:379) in that stalk is better developed, larger relative to size of processes, length of stalk in my specimen (Fig. 2) 2.8 as opposed to 2.1 mm. in Hamilton's specimen; median process shorter, 1.5 as opposed to 1.8 mm., proximal end rounded rather than concave, not partially enclosing tip of shaft; proportion of and relative sizes of median and lateral processes approximately same as in Hamilton's *Lemmus helvolus* [= *Lemmus trimucronatus helvolus*].

A specimen figured by Dearden (1958:542) has a basally trilobed median process.

The baculum of the Asiatic *Lemmus lemmus* figured by Ognev (1948:413) agrees with my specimens in the ossification of three processes, the relative sizes of these processes to each other and to the stalk, the well-developed base of the stalk and heavy bluntly rounded shaft; the baculum of *Lemmus lemmus* differs in greater anterolateral extent of basal tuberosities, in proximal notch seemingly separating these tuberosities, and in median process being slenderer.

Specimens examined: Five, of two subspecies; *Lemmus trimucronatus alascensis,* Point Barrow, Alaska, numbers 50591, 50678, 50731, 50758; *Lemmus trimucronatus subarcticus,* Wahoo Lake, 69°08′, 146°58′, 2350 ft., Brooks Range, Alaska, 50948.

Synaptomys cooperi Baird

Figs. 5 and 6

Baculum: Stalk elongate, greatest length (2.7 to 2.8 mm.) 2⅓ to 2½ times greatest breadth, 4 to 5 times greatest depth; three processes ossified or lateral processes unossified, ossifications relatively small (in 78380, median ossification less than ¼ as large as lateral ossifications although median cartilaginous process is larger), length of median process ⅕ to ⅙ of length of stalk, cartilaginous part of median process larger; posterior profile in dorsal view convex throughout or bilobate; tuberosities moderately developed, deflected dorsal to axis of shaft; in end-view medial construction ⅗ greatest depth of tuberosities; shaft tapered from point of greatest width, slightly inflated terminally.

The specimen (KU 13716) figured by Hibbard and Rinker (1942:29) has been restudied. It was first cleared and stained to soften the dry cartilage binding the digital processes together and to differentiate bone and cartilage. The lateral processes are small and cartilaginous (Fig. 6) and seem intact. The differences between this specimen and others examined by Hamilton (1946: 381), Dearden (1958:542), and myself, namely the relatively larger median ossification, the absence of ossification in lateral processes, and the distinctly bilobate base and larger size, may represent geographic differences, or individual variation. The proportions of length, width, and depth of the stalk, and the appearance in lateral view do not differ greatly from others examined by Hamilton, by Dearden (1958:546), and by me.

Specimens examined: Five, representing four subspecies; *S. cooperi gossii,* 6 mi. N Midway, Holt Co., Nebraska 78379, 78380; *S. cooperi relictus,* 5 mi. N, 2 mi. W Parks, Dundy Co., Nebraska, 72601 (immature); *S. cooperi saturatus,* 3 mi. S Demotte, Jasper Co., Indiana, 3-C-454, collection of W. B. Quay; *S. cooperi paludis,* Meade County State Park, Kansas, 13716.

Clethrionomys rutilus Pallas

Fig. 11

Baculum: Stalk elongate, and proximally enlarged, greatest length (2.7 mm.) 2 times greatest breadth; less than 4 times greatest depth; three well-developed ossified processes; length of stalk 2⅓ times length of median process; median process with basal (and ventral) protuberence and lateral lobes, arched in dorsoventral plane; lateral processes as large as median process, flattened distally, having ventromedial vane on distal half; basal tuberosities of stalk well developed, medially confluent; posterior profile in dorsal view trilobate or convex

throughout with rounded posterior apex; dorsal concavity well developed, ventral surface but slightly concave, medial constriction of base as little as ½ greatest depth; shaft straight, slender, at mid-point of stalk but slightly wider than high; basal tuberosities largely dorsal to axis of shaft in lateral view; lateral profile in dorsal view with an abrupt curvature separating the gently sloping sides of the shaft from the basal part at its greatest breadth.

The specimen of *Clethrionomys rutilus* figured by Ognev (1950:120) is essentially like the North American specimens examined by me in the relative sizes of the ossifications and the general shape of the stalk.

Specimens examined: Four, of one subspecies; *C. r. dawsoni*, west bank Gakona River, 1700 ft., 5 mi. NNE Gulkana, Alaska, 42865, 42866; SW end Dezadeash Lake, 2400 ft., Yukon Territory, 42910, 42921.

Clethrionomys gapperi (Vigors)

Fig. 10

Baculum: Stalk elongate, greatest length (2.8 mm.) 1¾ times greatest breadth, and 3¾ times greatest depth; proximally enlarged, greatest depth ½ greatest breadth; three well-developed ossified processes; length of stalk 2⅓ times length of median process; median process arched in dorsoventral plane, with basiventral protuberence or spine and lateral lobes; lateral processes as large as median process, flattened distally, arched; basal tuberosities of stalk well developed, medially confluent; posterior profile in dorsal view trilobate or convex throughout with a rounded posterior apex; dorsal concavity well developed, ventral surface but slightly concave, or in some cases slightly convex; medial constriction of base ⅗ greatest depth; shaft straight, slender, at mid-point of stalk twice as wide as high; basal tuberosities dorsally placed relative to axis of shaft; lateral profile in dorsal view abruptly curved anterior to point of greatest width; slender stalk distinct from angular enlarged base.

The most noticeable difference between the baculum of *C. rutilus* and *C. gapperi* is size. The proportions of the four ossifications are approximately the same. Ventral vanes on the lateral processes are not developed in *C. gapperi*. *C. gapperi* and *C. rutilus* are more nearly alike in their bacula than any other two species of *Clethrionomys* examined. *Clethrionomys occidentalis*, the other New World species, is also much like *C. gapperi* and *C. rutilus*. The differences are of a magnitude comparable to those between the bacula in subspecies of *Microtus montanus* (Figs. 19-21) for example, or in subspecies of *Lagurus curtatus* (Dearden, 1958:542).

Specimens examined: Nine, of two subspecies; *Clethrionomys gapperi athabascae*, British Columbia, 42922 (Indian Creek, Mile Post 234 of Alaskan Highway), 64281 (West bank Racing River, 89 mi. W Muskwa), 64287 (North bank Tetsa River, 56 mi. W, 11 mi. S Muskwa), 64290 (44 mi. W, 9 mi. S Muskwa), 64310 (32 mi. W, 2 mi. S Muskwa); *Clethrionomys gapperi galei*, 31 mi. N Pinedale, Sublette Co., Wyoming, 42108; Grand Mesa, Delta Co., Colorado, 60014 and 60015 (5½ mi. E, 12 mi. S Collbran), 60022 (8 mi. E, ½ mi. S Skyway).

Clethrionomys occidentalis (Merriam)

Fig. 12

Baculum: Stalk elongate, greatest length (2.8 mm.) 2½ times greatest breadth, 6 times greatest depth; three well-developed ossified processes; median process larger than lateral processes, ½ the length of stalk, curved, basally

broad, ventrally keeled, trilobate posteriorly; lateral ossifications large, flattened distally, curved; posterior profile of stalk posteriorly slightly emarginate, thus bilobate in outline; in end-view dorsal concavity deeper than ventral, constriction less than ½ greatest depth, tuberosities confluent, visible in dorsal view at each side; shaft slender, especially in depth, straight; at mid-point of stalk almost twice as wide as deep, slight terminal inflation.

The general proportions of the stalk and the relatively large, uniquely shaped processes, are characteristic of most specimens of the genus *Clethrionomys* examined.

Specimen examined: C. occidentalis californicus, one from Mary's Peak, Benton Co., Oregon, 30, F. W. Sturges' collection.

Clethrionomys glareolus Schreber

Fig. 13

Baculum: Stalk elongate, greatest length (2.9 mm.) twice the greatest breadth in the specimen examined, flattened proximally, greatest length almost 6 times greatest depth of base; three well-developed ossified processes; median process arched in a dorsoventral plane, with basal notch and lateral lobes; lateral processes as long as median process, bowed in dorsal view, flattened distally, with ventromedial vane; basal tuberosities of stalk weakly developed, medially confluent; posterior profile in dorsal view evenly rounded; in end-view dorsal concavity shallow in comparison to most species but deeper than ventral concavity, constriction ¾ greatest depth; shaft straight, at mid-point slightly wider than high, elongate, widest point of stalk less than ¼ of total length from proximal end, slight lateral inflation at tip; lateral profile in dorsal view sloping at first abruptly and then gradually from widest point of stalk anteriorly onto shaft.

The specimen of *Clethrionomys glareolus* figured by Ognev (1950:31) in dorsal view as I interpret it, resembles my specimen in the rounded base; in the elongate, distally inflated shaft; in the initially abrupt slope of the lateral profile in dorsal view from the greatest width of stalk anteriorly; and in the presence of three well ossified processes. Ognev's specimen differs from mine in the median process being more elongate relative to its width, and rounded proximally, lacking lateral lobes and basal notch; in lateral processes being less curved; in the greater terminal inflation of the shaft; and in the closer approximation of the terminal processes to the shaft. The baculum of *Clethrionomys glareolus* as described and figured by Didier (1954:243-244) resembles my specimen in general proportions, but is more pointed proximally and more curved in dorsoventral plane. Didier states that the baculum is rather variable in form in this species, in different regions, but that a large number of specimens must be examined to assess the geographic nature of this variation.

Specimen examined: One from Zermatt, Valais, Switzerland, 67100.

Clethrionomys rufocanus Sundevall

Fig. 9

Baculum: Base of stalk broad but relatively flattened dorsoventrally, greatest length (3.2 mm.) less than 1½ greatest width, 4 times greatest depth; three well-developed ossified processes; median process arched in dorsoventral plane, having basal notch and lateral lobes; lateral processes as long as median process,

flattened distally, with ventromedial vane; basal tuberosities of stalk weakly developed, medially confluent; posterior profile in dorsal view convex with rounded posterior apex; dorsal surface of base almost flat, ventral concavity broad and shallow; constriction ¾ greatest depth (not including an unusual irregularity on the ventral surface of the base); shaft straight, at mid-point of stalk distinctly wider than high, slender at distal end, widest point of stalk almost ⅓ of total length from proximal end, tip of shaft rounded; lateral profile in dorsal view gradually sloping from widest point anteriorly onto shaft.

The specimen of *Clethrionomys rufocanus* figured by Ognev (1950:97) resembles my specimen in the presence of three well ossified processes. Ognev's specimen differs however in the lack of a proximal notch on the median process, the lesser proportion of the stalk included in the basal enlargement, the more posterior position of the point of greatest width, and the presence of a concavity in the posterior profile of the stalk in dorsal view. These differences in the stalk may be owing to a difference in age (my specimen perhaps being older).

Specimen examined: One from 1 mi. NW Oho-ri, 6 M., Korea, 60438.

Phenacomys intermedius Merriam

Figs. 7 and 8

Baculum: Stalk slender, greatest length (2.9 mm.) 2¼ to 2½ times greatest breadth, 4 times greatest depth; three well-developed ossified processes, median one almost ½ length of stalk, curved, broad basally and slightly larger in all dimensions than either lateral process; lateral processes flattened distally, curved; base of stalk well developed, basal tuberosities medially confluent or separated by medial emargination, posterolateral faces flattened or rough; emarginations in the four adults examined; posterior profile in dorsal view bluntly pointed or flattened except for emargination posterially, abruptly curved at point of greatest width; shaft arising broadly from distal side of base of stalk; in end-view hour-glass shaped, medial constriction pronounced, both dorsal and ventral concavities deep; shaft having relatively straight but distally convergent sides; at mid-point of stalk, 1 to 1½ times as wide as deep; tip bluntly rounded, or slightly inflated.

The specimens from Quebec differ from the one from Wyoming in smaller size, relatively smaller lateral digital processes, larger more medial basal emargination, and slender shafts. The baculum of *Phenacomys intermedius* differs much from that of *Phenacomys longicaudus,* described by Hamilton (1946:381) and by Dearden (1958:547). Dearden states that the three bacula examined by him of *Phenacomys longicaudus* differ markedly from the specimen described by Hamilton. It seems to me that in major features the resemblance is greater between the specimens of *Phenacomys longicaudus* examined by these two authors than between their specimens and specimens of other microtines, including *Phenacomys intermedius.* Neither Hamilton nor Dearden record the exact localities of capture, the collections in which the specimens are deposited, or the catalogue numbers of specimens. Consequently verification of identifications and observations is difficult.

Specimens examined: Five, of two subspecies; *P. intermedius intermedius,* 5.4 mi. S Moran, Teton Co., Wyoming, 3-C-309, collection of W. B. Quay; *P. intermedius celatus,* four (including one immature specimen) from Authier-

nord, Abitibi-ouest Co., Quebec, specimens in collection of Bristol Foster designated by numbers 2041-2044 of S. Anderson's field catalogue. Smith and Foster (1957:107) were of the view that *Phenacomys ungava* (including the above specimens from Quebec) may be specifically distinct from *Phenacomys intermedius.*

Ondatra zibethicus (Linnaeus)

Not figured

Baculum: In the single specimen examined, less mature than that figured by Hamilton (1946:384), the digitate processes are cartilaginous, the basal tuberosities are less well developed, and the shaft is slenderer throughout. The cartilaginous processes are of the same proportions as ossified processes in the figure mentioned. The shaft is also convex ventrally in lateral profile. The view of the side here considered to be anatomically the ventral side (adjacent to the urethra) is labelled dorsal view in Hamilton's specimen.

Specimen examined: One, from Reserve, Brown Co., Kansas, 72405.

Microtus (Herpetomys) guatemalensis Merriam

Figs. 42 and 43

Baculum: Stalk moderately elongate, greatest length (3.5 mm.) 2⅓ times greatest breadth, spatulate, flattened throughout, greatest thickness ⅓ millimeter; three ossified processes; median process having three cornered base, curved dorsally, wider than high, ¼ to ⅕ greatest length of stalk; each lateral process bent at middle, as long as median process, compressed laterally; base of stalk curved dorsally, tuberosities marginal, hence narrow, lateral excavations of tuberous margin not confluent medially; in end-view ventral concavity broad, no dorsal concavity, medial constriction but slightly less than greatest thickness (not depth); shaft wider than high throughout, at mid-point more than 3 times as wide as high; tip of shaft slightly inflated both laterally and dorsoventrally; lateral profile gradually sloping anteriorly from widest point of stalk.

Specimen number 65921 (Fig. 43) differs from number 65895 (Fig. 42) described above. Terminus of shaft of number 65921 has lateral lobes from which arise lateral cartilaginous processes; median terminal ossification irregular in shape, smaller, imbedded in terminally bilobate cartilage. In the spatulate flattened stalk these two specimens are much alike. An immature specimen, number 65908, is smaller (length of stalk 2.6 mm.) also flattened and spatulate, has the terminal processes cartilaginous, the lateral processes bent medially, and proportions as in the adult.

The baculum shows no noteworthy resemblance to that of any other species of North American *Microtus;* on the other hand the differences between *M. guatemalensis* and some other species are no greater than the differences between certain species included in the subgenus *Microtus.* The baculum neither strengthens nor weakens the case for subgeneric rank for *M. (Herpetomys) guatemalensis.*

Specimens examined: Three from Guatemala; 65895 (2 mi. S San Juan Ixcoy), 65908, (3½ mi. SW San Juan Ixcoy), 65921 (10 mi. E, 4 mi. S Totonicapán).

Microtus (Arvicola) richardsoni (DeKay)

Figs. 38 and 39

Baculum: Stalk broad, greatest length (3.7 to 4.3 mm.) 1½ times greatest breadth, relatively flattened, greatest depth ⅓ greatest breadth; single median ossified process, in smaller of two specimens this ossification incomplete and of unusual shape (Fig. 39); length of stalk 4 times length of median process; concavities of basal tuberosities medially confluent, constriction less than ½ greatest depth; widest point of shaft less than ¼ length of shaft from posteriormost point; shaft wider than high except at distal end that is inflated dorsally and sometimes laterally; both ventral and dorsal concavities of base of stalk broad and moderately deep; posterior profile in dorsal view evenly rounded or having marginal notch.

In the absence of ossified lateral processes my two specimens differ from bacula of *Microtus* (*Arvicola*) *terrestris* figured by Didier (1943:79, 1954:245, 247, 248) and by Ognev (1950:591). The median process relative to the size of the shaft is smaller, and the shaft relative to its length is wider in *M. richardsoni* than in *M. terrestris*. The stalk of *M.* (*Arvicola*) *amphibius* figured by Didier is like that of *M. richardsoni* in its greater breadth and median notch on posterior border.

The relationship of the New World water rat, *M. richardsoni*, to the Old World water rats (genus *Arvicola* of some European authors) is uncertain. Miller (1896:66) placed all of them in the subgenus *Arvicola*. Subsequent authors, stressing differences in the teeth, have placed *M. richardsoni* in the subgenus *Aulacomys* of Rhoads. Zimmerman (1955) has shown that teeth in some *Arvicola* approach the more complex pattern of *M. richardsoni*. He argues also that *Arvicola* is generically distinct from *Microtus* on the grounds that the two groups have separate origins, *Arvicola* having descended from the genus *Mimomys* and *Microtus* from some other group of microtines. This argument also was advanced by Hinton (1926:47-48). Pending further studies of the possible polyphyletic origin of other subgenera of the genus *Microtus*, I refer both *M. richardsoni* and *M. terrestris* to the subgenus *Arvicola*.

The evidence afforded by the bacula available is not conclusive as to relations of Old World and New World water rats. No general agreement on the number of species in this Palaearctic group has been reached, and bacula of only three or four of the numerous Old World subspecies have been figured. I have examined none.

Specimens examined: Two, from Wyoming; 42454 (31 mi. N Pinedale, 8025 ft., Sublette Co.), 37903 (23½ mi. S, 5 mi. W Lander, 8600 ft., Fremont Co.).

Microtus (Chilotus) oregoni (Bachman)

Fig. 45

Baculum: Stalk broad, greatest length (2.2 mm.) 1¾ times greatest breadth, 3½ times greatest depth; three well-developed ossified processes; median process ⅔ length of stalk, rounded or tapered terminally, proximal end opposed to tip of stalk and flattened obliquely; lateral processes ⅔ length of median process, deeper than wide, curved; tuberosities of stalk well developed, confluent medially, visible in dorsal view; in end-view dorsal concavity narrow, moder-

ately deep, rounded, ventral concavity wide, deep, flattened; base wider ventrally than dorsally; shaft tapering more or less uniformly, terminally inflated.

In the relative sizes, to each other and to the stalk, of the three digitate ossifications *M. oregoni* resembles closely the Old World representative of the same subgenus, *M.* (*Chilotus*) *socialis*, as figured by Argyropulo (1933b:181). In *M. oregoni* the greatest width of the baculum is more proximal on the stalk than in the *M. socialis* figured by Argyropulo but closely resembles the baculum of the *M. socialis* figured by Didier (1954:242). In possessing a shallow emargination in the base of the stalk and in possessing a median process that is smaller than the lateral processes, *M. socialis*, as figured by Didier, differs from *M. oregoni*. The baculum figured by Argyropulo (*loc. cit.*) of *Sumeriomys colchicus schidlovskii* [= *Microtus* (*Chilotus*) *socialis schidlovskii* according to Ognev, 1950:392] differs from other *Chilotus* that have been studied in having an unusually elongate median process and a more distal placement of the widest part of the stalk.

Specimens examined: Three, of the subspecies *M. oregoni oregoni*, from 5 mi. N Orick, Humboldt Co., California, 3-C-248, collection of W. B. Quay; from Mary's Peak, Benton Co., Oregon, 66, collection of F. W. Sturges; and from Sec. 3, T. 11S, R. 5W, Benton Co., Oregon, 79183.

Microtus (Stenocranius) gregalis (Pallas)

Fig. 34

Baculum: Length of stalk (2.4 mm.) 1¾ times greatest breadth, 4⅓ times greatest depth; median ossified process well developed, more than ⅓ length of stalk, higher than wide, slightly bowed, closely appressed to terminus of shaft; basal tuberosities of stalk moderately developed, confluent medially, posterior profile of medial apex rounded in dorsal view, lateral indentations present, hence trilobate outline; in proximal end-view base wider ventrally, ventral concavity broader than dorsal concavity but of equal depth, medial constriction ⅔ greatest depth; shaft slender in distal part, inflated terminally, and wider than high at mid-point of stalk; lateral profile a smooth slope of gradually decreasing curvature from point of greatest width to near distal end.

The baculum of this species figured by Ognev (1950:461) differs in having lateral ossified processes, and a more rounded base of the stalk. Resemblance to the New World *Stenocranius* is discussed below.

Specimen examined: One from "Eastern Europe," 8059.

Microtus (Stenocranius) miurus Osgood

Figs. 32 and 33

Baculum: Length of stalk (2.8 mm.) 1½ times greatest breadth, 3½ times greatest depth; median process ossified, ⅖ to ⅗ length of stalk, laterally compressed, sometimes arched in dorsoventral plane; lateral processes cartilaginous, slender; basal tuberosities well developed, averaging less enlarged than shown in Figure 32, but more angular in lateral outline than shown in Figure 33; tuberosities confluent posteriorly; posterior profile smoothly rounded to trilobate, curvature at point of greatest breadth usually acute; in proximal end-view base wider dorsally, deep dorsal concavity, shallow ventral concavity, medial constriction ⅗ of greatest depth; shaft slender anteriorly, at mid-point of stalk

twice as wide as high, at tip higher than wide, laterally inflated; lateral profile in most specimens abruptly curved anterior to point of greatest breadth.

The single specimen of the Old World *M.* (*Stenocranius*) *gregalis* examined resembles the New World *M.* (*Stenocranius*) *miurus* in the angular lateral profile at the point of greatest breadth of the stalk, slender shaft in comparison to broad base of stalk, and presence of a single well-developed laterally compressed median process. The base of the stalk in the baculum of *M. gregalis* is less well developed and smaller than in the baculum of *M. miurus*.

Specimens examined: Nine, all of the subspecies *Microtus miurus muriei*, from the Brooks Range, Alaska; 51077 (Lake Schrader, 145°09′50″, 69°24′28″, 2900 ft., Romanzof Mts.); 51151, 51152, 51154, 51164, 51166, 51169 (last 6 from Wahoo Lake, 69°08′, 146°58′, 2350 ft.); 51210, 51213 (last 2 from Porcupine Lake, 68°51′57″, 146°29′50″, 3140 ft.).

Microtus (Chionomys) nivalis Martins

Fig. 47

Baculum: Greatest length of stalk (2.7 mm.) 2¼ times greatest breadth, 4½ times greatest depth; three digitate processes, lateral processes mostly cartilaginous in single adult examined; median process well ossified, approximately ⅓ length of stalk, basally notched, not arched, laterally compressed distally; base of stalk broad and flat, basal tuberosities well developed, separate; posterior profile in dorsal view rounded, convex except for medial notch separating tuberosities; dorsal and ventral concavities deep, broad, equal; medial constriction less than ½ greatest depth; in dorsal view shaft tapering gradually from widest point, terminally rounded; at mid-point of stalk almost twice as wide as high.

In the elongate, largely cartilaginous lateral processes of the baculum, the specimen described above resembles *M. longicaudus*. The size of the median process in comparison to the size of the stalk is also the same. The lateral processes have larger ossifications and the base of the stalk is more robust in *M. longicaudus* than in *M. nivalis*.

The well ossified lateral processes and enlarged base of Didier's (1954:240) specimen suggest that it is of a more mature individual than the one described above. These specimens of *M. nivalis*, as well as the specimens of *M. longicaudus*, exhibit dorso-ventral flattening of the mid-part of the base of the stalk.

The baculum of a specimen from Switzerland is weakly developed, of small size (shaft 2.0 mm. in length), slender, thin, spatulate, and terminally inflated. Digital processes were not observed, perhaps owing to excessive maceration in preparation. The general appearance of the baculum is that of an immature individual, although the animal was not small (165 mm. total length in preservative).

Specimens examined: Two *Microtus nivalis nivalis*; Zermatt, Valais, Switzerland, 67105; Wetterstein, Germany, 65127.

Microtus (Chionomys) longicaudus (Merriam)

Fig. 48

Baculum: Base of stalk well developed, greatest length (3 mm.) 1¾ times greatest breadth, 3⅔ times greatest depth; three ossified processes; base of median process rounded; median process slightly curved in dorsoventral plane, in length almost ⅓ greatest length of stalk; ossifications in lateral processes

variable in size, frequently widely separated from shaft by cartilage, rarely as large as median ossification; basal tuberosities usually well-developed, medially confluent; profile of base in dorsal view trilobate or irregularly convex throughout; constriction ½ greatest depth; shaft relatively straight or slightly bowed ventrally or dorsally, shaft at mid-point of stalk wider than high; tip of shaft laterally inflated; widest point of stalk approximately ¼ length of stalk from proximal end; lateral profile in dorsal view tapers gradually onto shaft anteriorly from point of greatest width of stalk; shaft variable, from slender terminally and nearly parallel sided (Fig. 48), to broad distally and tapered.

In many of the features that distinguish *M. longicaudus* (and the closely related insular species *M. coronarius*) from other North American *Microtus, longicaudus* resembles the Old World species of the subgenus *Chionomys* (that is to say, *M. nivalis, M. gud,* and *M. roberti*). These features are medium size, long tail, grayish color, montane habitat, relatively short molar tooth-row, moderate sized and unconstricted incisive foramen, relatively decurved upper incisors, elongate nasals, relatively broad interorbital region without well-developed median ridge, and similar chromosomes (Matthey, 1955:178). For these reasons I am here referring *Microtus longicaudus* to the subgenus *Chionomys;* previously it has not been referred to that subgenus.

Specimens examined: Six, of three subspecies; *Microtus longicaudus littoralis,* Sullivan Island, Alaska, 42972, 42969; *M. l. mordax,* ¾ mi. N, 2 mi. W Allenspark, 8400 ft., Boulder Co., Colorado, 50335, 76829; *M. l. sierrae,* Crane Flat, Mariposa Co., California, 50252, 50253.

Microtus arvalis (Pallas)

Fig. 22

Baculum: In the single specimen examined, stalk small, greatest length (2.3 mm.) 2⅓ times greatest width, almost 6 times greatest depth, flattened proximally; three well-developed digitate processes, the median one ossified, the lateral processes cartilaginous; median ossification laterally compressed and decurved at tip, bilobate at base; basal tuberosities of stalk weakly developed, medially confluent; posterior profile in dorsal view evenly rounded; ventral concavity deeper and narrower than dorsal concavity, but both comparatively shallow; medial constriction ⅔ greatest depth; shaft straight, at mid-point twice as wide as deep; lateral profile tapering from greatest width gradually to parallel sides of distal third of stalk.

From the baculum of *Microtus arvalis* figured by Ognev (1950:173), and from the baculum figured by Didier (1954:238) my specimen differs in the absence of lateral ossifications in the digitate processes, smaller and slenderer median ossification, and weaker base. These differences in part may be owing to a difference in age, my specimen being the less mature.

Specimen examined: One from Vidy, Switzerland, 67101.

Microtus orcadensis Millais

Fig. 24

Baculum: In the one specimen examined, stalk broad, greatest length (2.6 mm.) 1½ times greatest breadth, 3½ times greatest depth; three digitate processes ossified; median process relatively broad, in length more than ½ length of stalk, triangular in dorsal view, with small spurs posterolaterally,

middorsal ridge posteriorly; lateral ossifications slightly curved, slenderer, less than ½ depth and less than ½ transverse thickness of median process; basal tuberosities well-developed, confluent medially; in end-view base wider dorsally than ventrally, dorsal concavity broader and more abruptly curved at mid-point than ventral concavity; constriction ½ greatest depth; posterior profile in dorsal view notched, setting off a posterior shelf; stalk including shaft wider than deep throughout, at mid-point width twice depth; lateral profile abruptly curved anterior to point of greatest width, sides of shaft tapering gradually anteriorly to rounded uninflated tip.

The baculum of this insular species, placed in the *"arvalis"* group by Ellerman (1941:595), resembles the baculum of both *Microtus agrestis* and *Microtus guentheri* more than it resembles the baculum of *Microtus arvalis*. Similarities in the chromosomes of *M. arvalis* and *M. orcadensis* were noted by Matthey (1953:254, 279), who was of the opinion that *M. orcadensis* is an insular derivative of the *arvalis*-group.

Specimen examined: One from the Orkney Islands, 67106.

Microtus guentheri Danford and Alston

Fig. 23

Baculum: In the one specimen examined, stalk broad, greatest length (2.9 mm.) 1½ times greatest breadth, 3½ times greatest depth; three digitate processes ossified; median process slightly less than ½ length of stalk, broad, dorsally curved; curved lateral ossifications shorter and more slender than median ossification; basal tuberosities well developed, angular, confluent across posterior border of projecting shelf; in end-view tuberosities projecting ventrolaterally from central shelf; dorsal surface at medial constriction flat, ventral surface broadly and deeply concave; posterior profile in dorsal view trilobate, central lobe formed by posteriorly flattened shelf, surface of attachment visible only on lateral lobes; at mid-point stalk almost twice as wide as deep, depth of shaft greater than width proximal to inflated terminus.

Specimen examined: One from Palestine, 67104.

Microtus fortis Büchner

Fig. 25

Baculum: Stalk large, greatest length (3.8 mm.) 1⅘ times greatest breadth, 4½ times greatest depth; three digitate processes ossified; median ossification almost ⅓ length of stalk; lateral ossifications slender, smaller than median ossification; posterior profile of stalk in dorsal view trilobate, basal tuberosities well developed, confluent medially; in end-view dorsal concavity broader and deeper than ventral concavity; medial constriction pronuonced (less than ½ greatest depth); lateral profile at widest point of stalk convex, becoming abruptly concave as the flange of the basal tuberosities grades into the shaft, then gradually converging to narrowest point ⅓ of length of stalk from the terminus; stalk wider than deep in proximal ⅔, circular in cross section in terminal ⅓, slight terminal inflation.

A specimen figured by Ognev (1950:297) has the same general proportions, slender lateral processes, and proximal placement of the point of greatest breadth.

Specimens examined: Two from Chipo-ri, Korea, 60443, 63841.

Microtus montanus (Peale)

Figs. 19, 20 and 21

Baculum: Stalk broad, greatest length (varying with subspecies from 2.3 to 3.1 mm.) 1½ to 1¾ times greatest breadth, 3½ to 4⅓ times greatest depth; three ossified processes, median one largest, more than twice as wide and as deep as shorter, slenderer, lateral processes; median process laterally compressed distally except in one specimen in which moderately inflated distally, proximally enlarged in some specimens (Fig. 21) and ⅛ to ⅖ length of stalk; base broad, posterior profile in dorsal view evenly convex throughout, at widest point of stalk abruptly incurved; basal tuberosities moderately to strongly developed, medially confluent; in end-view base wider ventrally than dorsally, dorsal concavity slightly to much deeper than the nearly flattened ventral concavity; medial constriction ⅔ to ⅘ of greatest depth; shaft relatively slender, at mid-point of stalk slightly wider than high and ¼ as wide as base of stalk, terminally rounded or slightly inflated; lateral profile in dorsal view a gradual curve from point of greatest width anteriorly onto shaft.

The different subspecies figured show the essential characteristics of the species, differing primarily in size.

Specimens examined: Fourteen, of three subspecies; *Microtus montanus amosus,* ½ mi. E Soldier Summit, Wasatch Co., Utah, 62241; *M. montanus fusus,* La Manga Pass, Conejos Co., Colorado, 42164; 5 mi. N, 26 mi. W Saguache, 9500 ft., Saguache Co., Colorado, 42307, 42315; 5 mi. N, 27 mi. W Saguache, 9350 ft., Saguache Co., Colorado, 42308; 5 mi. N, 28 mi. W Saguache, 9325 ft., Saguache Co., Colorado, 42309; 5 mi. S, 24 mi. W Antonito, 9600 ft., Conejos Co., Colorado, 42327, 42330; Prater Canyon, Mesa Verde National Park, Montezuma Co., Colorado, 69456, 69457, 69463; *Microtus montanus nanus,* 2 mi. N, 2 mi. W Pocatello, Bannock Co., Idaho, 57470, 57472; ¾ mi. N, 2 mi. W Allenspark, 8400 ft., Boulder Co., Colorado, 50330.

Microtus townsendii (Bachman)

Fig. 41

Baculum: Stalk broad, greatest length (3.0 mm.) 1½ times greatest breadth, 4½ times greatest depth; three ossified processes, median one largest, deeper and more than twice as wide as curved, shorter, compressed lateral processes and more than ⅔ as long as stalk; base broad, in dorsal view posterior profile trilobate, basal tuberosities visible; basal tuberosities well developed, medially confluent; in end-view base wider ventrally than dorsally, dorsal concavity deeper than ventral concavity; medial constriction ⅗ of greatest depth; shaft broad, at mid-point more than twice as wide as high and ⅓ as wide as base of stalk, terminally rounded.

Specimens examined: Three, all *M. t. townsendii;* Fort Lewis, Pierce Co., Washington, 57998, subadult; Sec. 33, T. 11S, R. 5W, Benton Co., Oregon, 79186; Sec. 5, T. 12S, R. 4W, Benton Co., Oregon, 79188.

Microtus oeconomus (Pallas)

Fig. 44

Baculum: Stalk broad and flattened, greatest length (3.5 mm.) 1⅔ to 2 times greatest width, 4 to 5½ times greatest depth; three ossified processes, median one largest, lateral processes slender, relatively small; length of median process ⅝ length of stalk; median process decurved, dorsoventrally flattened in

some specimens, widened at base; attachment of processes to shaft displaced ventrally; base of stalk widened, posterior profile in dorsal view usually trilobate, in a few cases rounded, median lobe forming posterior shelf, lateral lobes dorsally raised and forming margins of lateral tuberosities; in end-view thickness frequently more or less uniform throughout central part, broad depression dorsally, ventral concavity narrower and shallower (as figured); base, and occasionally shaft, flattened, width at mid-point of stalk 2 to 3 times depth, narrowest point posterior to terminal inflation of shaft in terminal ⅓ of shaft.

The baculum of *M. oeconomus* (Old World) figured by Ognev (1950:257) resembles but exceeds that of *M. oeconomus* (New World) in the relatively large median process and slender lateral processes, but differs noticeably in the presence of a deep median notch in the base of the stalk. A specimen from Hungary is intermediate between Ognev's specimen and those from the New World in both size of median process and size of lateral processes, and has an unnotched base resembling that in Figure 44.

Specimens examined: Ten, of three subspecies; *M. oeconomus gilmorei,* Umiat, Alaska, 51354, 51361, 51399, 51408; Lake Schrader, Brooks Range, Alaska, 51422; *M. o. macfarlani,* 5 mi. NNE Gulkana, Alaska, 43039, 43041; 20 mi. NE Anchorage, Alaska, 43044; Kelsall Lake, British Columbia, 43048; *M. o. mehelyi,* Kisbalatan, Hungary, 75159.

Microtus mexicanus (Saussure)

Figs. 35 and 36

Baculum: Stalk attenuate, greatest breadth relatively near proximal end; greatest length (3.1 to 3.4 mm.) more or less twice greatest breadth, 4 to 5 times greatest depth; usually a single process ossified; lateral processes relatively small, cartilaginous or (in three specimens, 63094, 69453, 68019) with small ossifications; median process relatively small, sometimes appressed to tip of shaft, in length less than ¼ length of stalk; posterior profile in dorsal view rounded, flattened posteriorly, or in some specimens trilobate with angular edges; in end-view relative depths of dorsal and ventral concavities variable, dorsal usually deeper than ventral; distal end of stalk frequently bowed dorsally; shaft slender distally, sometimes slightly inflated terminally, or (in one specimen, 63085) near tip small lateral projections that are perhaps fused lateral ossifications; lateral profile in dorsal view a gradual slope anteriorly from point of greatest width to slender tip.

Specimens examined: Thirteen, of four subspecies; *Microtus mexicanus mexicanus,* Las Vigas, Veracruz, 30692; Nevada de Toluca, México, 63101; Valle de Bravo, México, 63094; *Microtus mexicanus mogollonensis,* Mt. Taylor, Valencia Co., New Mexico, 63298, 76830; Park Well, Mesa Verde National Park, Montezuma Co., Colorado, 69448, 69453; Upper Nutria, McKinley Co., New Mexico, 69997, 70000; *Microtus mexicanus phaeus,* Sierra Patamba, 9000 ft., Michoacán, 63085; *Microtus mexicanus subsimus,* 2 mi. E Mesa de Tablas, Coahuila, 58916; 13 mi. E San Antonio de las Alazanas, Coahuila, 68019, 68021.

Microtus californicus (Peale)

Fig. 37

Baculum: Stalk elongate, greatest length (3.0 mm.) 2⅓ times greatest breadth, 4½ times greatest depth; median process ossified, ¼ length of stalk, basally broadened, flattened and shallowly grooved ventrally to fit tip of shaft, to which the process is closely appressed; lateral processes cartilaginous; ends

of stalk bowed upwardly; posterior profile of base of stalk rounded or slightly trilobate if posterolateral concavities form in tuberosities; moderate development of tuberosities, in end-view dorsal concavity slightly deeper and narrower than ventral concavity, both comparatively shallow, median constriction ⅘ greatest depth; shaft curved, more or less terete at mid-point of stalk, terminally inflated dorsally; lateral profile in dorsal view gradually curved from point of greatest width anteriorly onto shaft.

Specimens examined: Two, of two subspecies; *Microtus californicus californicus*, 1 mi. NE Berkeley, in Contra Costa Co., California, 76828; *Microtus californicus mohavensis*, ½ mi. SE Victorville, San Bernardino Co., California, 63745.

Microtus pennsylvanicus (Ord)

Figs. 14, 15, 16 and 17

Baculum: Stalk heavy, broad, greatest length (2.2 to 3.0 mm.) 1⅓ to 1⅔ times greatest breadth, up to 3¾ times greatest depth; three ossified processes, median one largest, usually not twice so deep as lateral ossifications; median process usually distinctly widened basally, in length approximately ½ length of stalk; base broad, frequently angular laterally and basally, sometimes bilobate; basal tuberosities well developed, medially confluent; in end-view more or less uniformly biconvex or ventral surface more flattened than dorsal surface, medial constriction ½ to ⅔ greatest depth; shaft relatively heavy, at mid-point stalk almost twice as wide as deep and ⅓ as wide as base of stalk; shaft terminally rounded and sometimes slightly inflated; lateral profile in dorsal view abruptly or gradually curved anterior to point of greatest width and then gradually curved anteriorly.

Specimens examined averaged slightly smaller and were more variable than those described by Hamilton (1946:382). The greater variation may be in part geographic, as five subspecies are represented. Lateral processes are the last to ossify. One specimen (75082) with well-ossified median process lacks any lateral ossification. Four bacula of *M. pennsylvanicus* (locality not specified) studied by Dearden (1958:547) agree in general with the description above.

One specimen shows a break, perhaps resulting from injury, in the shaft (Fig. 14). One specimen has a posteromedian spine on the median digital ossification (Fig. 16). Comparison with *M. agrestis* is included with the description of *M. agrestis*.

Specimens examined: Thirteen, of six subspecies; *Microtus pennsylvanicus alcorni*, 20 mi. NE Anchorage, Alaska, 43043; *Microtus pennsylvanicus finitus*, Laird, Yuma Co., Colorado, 68544; *Microtus pennsylvanicus modestus*, 5 mi. N, 26 mi. W Saguache, 9500 ft., Saguache Co., Colorado, 42306; 3 mi. N, 16 mi. W Saguache, 8500 ft., Saguache Co., Colorado, 42416, 42417, 42418; 1 mi. S, 2 mi. E Eagle Nest, 8100 ft., Colfax Co., New Mexico, 42430, 42439; *Microtus pennsylvanicus pennsylvanicus*, 2 mi. S, 3 mi. E Ft. Thompson, 1370 ft., Buffalo Co., South Dakota, 42379; Vermillion, Clay Co., South Dakota, 37070; *Microtus pennsylvanicus pullatus*, 12 mi. S, 5 mi. E Butte, Silver Bow Co., Montana, 57501, 57503; *Microtus pennsylvanicus uligocola*, Muir Springs, 2 mi. N, 2½ mi. W Ft. Morgan, Morgan Co., Colorado, 75082.

Microtus agrestis (Linnaeus)

Fig. 18

Baculum: Greatest length of stalk (2.9 mm.) twice greatest breadth, 4½ times greatest depth; stalk well developed, shaft not flattened dorsoventrally; large median ossified process, minute lateral ossifications in single specimen

examined; length of stalk 2½ times length of median ossification which is higher than wide, slightly decurved, sagittate in dorsal view, with three-cornered base; basal tuberosities of stalk moderately well developed, medially joined; posterior profile in dorsal view evenly rounded; ventral concavity broader than, but of comparable depth to, dorsal concavity in end-view, base of stalk wider ventrally, constriction ¾ greatest depth; at mid-point of stalk shaft is but slightly wider than high; pronounced terminal inflation of shaft; lateral profile in dorsal view sloping abruptly from widest point of stalk anteriorly onto stalk which then tapers more gradually to terminal inflation.

From the baculum of its New World counterpart, namely *Microtus pennsylvanicus*, my specimen of *Microtus agrestis* and the specimen figured by Didier (1954:239) differ in their minute lateral processes, relatively larger median processes, and more elongate, less dorsoventrally flattened shafts.

The specimen of *M. agrestis* figured by Ognev (1950:320), in dorsal view has lateral concavities producing a somewhat trilobate outline in the base of the stalk, and the lateral processes are well developed; the median process is larger and bulbous, wider distally than proximally. Without larger numbers of bacula of *M. agrestis* I am unable to reconcile these differences. The differences between *M. agrestis* and *M. pennsylvanicus* seem comparable to the differences between some other species of *Microtus*.

Specimen examined: One, from Gryon, Switzerland, 67102.

Microtus (Pedomys) ochrogaster (Wagner)

Fig. 31

Baculum: Stalk broad, greatest length (3.2-4.0 mm.) 1⅔ to 2 times greatest breadth, 2½ to 4 times greatest depth; median process ossified, relatively small, less than 3/10 length of stalk; lateral processes arising from subterminal part of stalk, cartilaginous or with small ossifications; posterior profile in dorsal view broadly rounded or slightly angular, widest point of stalk ⅓ to ¼ the length of stalk from base; basal tuberosities well developed and medially confluent, in end-view dorsally convex, or at least less deeply concave than ventrally; shaft straight, base bent ventrally or more commonly dorsally; at mid-point of stalk wider than high, often twice as wide as high; viewed from above, lateral profile from point of greatest breadth to middle of shaft a gradual sigmoid curve; slight terminal inflation of shaft.

Specimens examined: Forty-one, of three subspecies; *Microtus ochrogaster haydeni*, Muir Springs, 2 mi. N, 2½ mi. W Ft. Morgan, Morgan Co., Colorado, 74995, 74998, 74999, 75002; 1 mi. W Laird, Yuma Co., Colorado, 57304, 76833; 2 mi. N, 2 mi. W Haigler, Dundy Co., Nebraska, 75016; 2 mi. S Franklin, Franklin Co., Nebraska, 75043, 75044; Atwood, Rawlins Co., Kansas, 75020, 75023, 75025, 75027, 75028; 1 mi. N, 2 mi. E Oberlin, Decatur Co., Kansas, 75030, 75032, 75034, 75035, 75036; 1½ mi. N, ¼ mi. E Norton, Norton Co., Kansas, 68327; 1 mi. SW Norton, Norton Co., Kansas, 75037; 2 mi. S, 1 mi. W Norton, Norton Co., Kansas, 75038; *M. ochrogaster ochrogaster*, Rydal, Republic Co., Kansas, 75047-75053, 75060, 75062, 75063, 75066, 75070, 75071, 75073; 1 mi. N, 1 mi. W Holton, Jackson Co., Kansas, 75077; 2 mi. W Court House, Lawrence, Douglas Co., Kansas, 76832; Univ. Kansas Natural History Reservation, Douglas Co., Kansas, 68536; *M. ochrogaster taylori*, Meade County State Park, Kansas, 68539, 68542.

Microtus (Pitymys) pinetorum (LeConte)

Figs. 27 and 28

Baculum: Stalk broad, greatest length (2.5 to 2.7 mm.) 1⅔ times greatest breadth, 4 times greatest depth; median process ossified, size small, ⅕ length of stalk, higher than wide, having small anterodorsal prominence in both specimens examined; lateral processes cartilaginous, relatively small, displaced posteriorly, attenuate; posterior margin in dorsal view broadly rounded, or having blunt median apex, convex throughout; basal tuberosities moderately well developed, medially confluent, barely visible in dorsal view when mature; in end-view median constriction ⅕ greatest depth, ventral concavity deeper than dorsal concavity, both comparatively shallow; stalk at mid-point 1½ times as wide as deep; shaft relatively slender, bowed dorsally at tip, relatively straight otherwise; lateral profile in dorsal view a gradual concave slope from point of greatest width anteriorly to distal part of shaft.

Specimens examined: Two, from Douglas Co., Kansas, 76834 (2 mi. N Baldwin), 68545 (1 mi. NE Pleasant Grove).

Microtus (Pitymys) parvulus (Howell)

Fig. 40

Baculum: Stalk broad, greatest length (2.4 mm. in specimen examined) 1¾ times greatest breadth, 4 times greatest depth; median process ossified, size small, less than ¼ length of stalk, wider than high, terminally flattened; lateral processes cartilaginous, relatively small, attenuate; posterior margin in dorsal view flattened, irregularly curved with concavities medially and laterally; basal tuberosities well developed, medially confluent; visible in dorsal view; in end-view median constriction ⅔ greatest depth, ventral concavity well-formed, no dorsal concavity; stalk at mid-point twice as wide as deep; shaft relatively slender, bowed dorsally toward tip; in dorsal view lateral profile a gradual concave slope from point of greatest width anteriorly to distal part of shaft; tip of shaft enlarged.

The baculum of *M. parvulus* resembles that of *M. pinetorum* more than it resembles the baculum of any other microtine studied, differing primarily in smaller size.

Specimen examined: One, from 1 mi. W Micanopy, Alachua Co., Florida, Univ. Florida No. 1508.

Microtus (Pitymys) quasiater (Coues)

Figs. 29 and 30

Baculum: Stalk broad, greatest length (2.6-3.2 mm.) 1⅓ to 1⅔ times greatest breadth, 3⅓ to 3⅔ times greatest depth; median process ossified, with ventral depression, process ¼ to ⅓ length of stalk, appressed to tip of shaft, wider than high proximally, relatively broad terminally; lateral processes cartilaginous, small, attenuate; posterior profile of stalk in dorsal view broadly rounded, bilobate, or trilobate, median lobe formed by posterior projection of dorsal shelf between enlarged lateral tuberosities that form outer lobes, posterolateral faces of these tuberosities visible in dorsal view of stalk; in end-view dorsal surface slightly concave, ventral concavity broad and deep, median con-

striction ½ greatest depth; shaft flattened except tip that is more terete, and bowed dorsally; at mid-point, stalk twice as wide as high; shaft relatively slender terminally, narrower than median ossification.

The baculum of *M. quasiater* is the largest and has the best developed base and median process of the three American species of the subgenus *Pitymys*. The three species closely resemble each other in basic form.

Specimens examined: Five, all from Veracruz; Teocelo, 4500 ft., 30709, 30711; 4 km. N Tlapacoyán, 1700 ft., 24466; 5 km. N Jalapa, 4500 ft., 19869, 19878.

Microtus (Pitymys) fatioi (Mottaz)

Fig. 26

The baculum of a single specimen (KU 67103) of *M. fatioi* from Zermatt, Valais, Switzerland, was examined. The baculum is immature, as evidenced by its small size, slender stalk and absence of ossified processes, therefore no characterization is included.

The baculum of another Old World species of the subgenus *Pitymys*, *M. pyrenaicus* from France, figured and described by Didier (1954:242-243), differs from all New World *Pitymys* examined in processing ossified lateral processes.

The status of *Pitymys*, as a genus or as a subgenus, is uncertain. Hall and Cockrum (1953:448) considered the North American *Pitymys* and *Pedomys* as subgenera of *Microtus*. They did not state specifically the basis for this point of view, but mention the fact that these two subgenera (*Pitymys* and *Pedomys*) closely resemble each other cranially. These authors did not study nor comment upon the status of the Old World *Pitymys*. It may be asked whether the Old World and New World *Pitymys* have developed as fossorial *Microtus* independently, or from an ancestor common to both groups and not common to any other *Microtus*. Matthey (1955:202) found 62 chromosomes (2N) in both the New World *Pitymys pinetorum* and the Old World *Pitymys duodecimcostatus*. This suggests, but does not prove, common ancestry.

Neofiber alleni True

Fig. 49

Baculum: Stalk massive, greatest length (4.7 mm.) 1¾ times greatest breadth, 4 times greatest depth; ossification in digitate processes variable; in one (KU 27123) of two specimens examined lateral processes ossified and median process unossified, as in two specimens examined by Hamilton (1946: 379) from "southern Florida"; in my other specimen (KU 27268) that is possibly more mature, median process ossified although less deeply stained than lateral ossifications or stalk; posterior profile in probable dorsal view roughly rounded; in end-view probable dorsal concavity deep, ventral concavity broad but shallow, and with center convex; median constriction ⅗ greatest depth; shaft heavy, least depth ⅔ greatest depth of base; stalk, at mid-point, slightly wider than deep and more than ⅓ width of base; lateral profile in dorsal view sharply incurved distal to point of greatest breadth, shaft therefore relatively distinct from basal part of stalk; slight subterminal constriction; tip less reduced in the two specimens examined than in two figured by Hamilton. In preparation, the tissues that make it possible to distinguish

with certainty the dorsal and ventral surfaces of the baculum were removed in both specimens.

Specimens examined: Two, of the subspecies *Neofiber alleni alleni*, 2 mi. S Gainesville, Alachua Co., Florida, 27268; 1 mi. E Courtenay, Merritt Island, Brevard Co., Florida, 27123.

Lagurus curtatus (Cope)

Fig. 46

Baculum: Stalk slender, greatest length (2.5 mm.) 2 to 2⅔ times greatest breadth, 4 to 5 times greatest depth; three ossified processes; median one more than ⅓ length of stalk, curved dorsally toward tip, proximally flattened and having acute lateral angles in dorsal view, wider than deep except in distal half; lateral processes smaller than median one, slenderer, shorter, of approximately same depth, also curved dorsally; base of stalk well developed, basal tuberosities medially confluent, in part visible in dorsal view, in end-view wider ventrally than dorsally, dorsal and ventral concavities of equal depth and both wide, medial constriction ½ greatest depth; posterior profile in dorsal view broadly bilobate; lateral profile with abrupt transition from basal tuberosities to gradually converging, slightly curved sides of shaft; shaft terminally inflated.

Dearden (1958:543) described and figured the bacula of six subspecies of *Lagurus curtatus* and two Asiatic species, *Lagurus lagurus* and *Lagurus luteus*. He examined at least 34 specimens of *L. curtatus* and found geographic variation in size, breadth of shaft distally, and proportions of digital ossifications to each other and to the stalk. The description that I have given above pertains to *L. c. levidensis*.

The baculum of the Asiatic *Lagurus* (*Lagurus*) *lagurus* figured by Ognev (1950:554) agrees with that of *Lagurus* (*Lemmiscus*) *curtatus*, described here, in the relatively elongate shaft and slender stalk, the proportions of the processes, and the well-formed and moderately enlarged base of the stalk. The bacula of three *Lagurus lagurus* examined by Dearden (1958:545) were of older individuals than the specimen that Ognev figures and differ from it and from bacula of *Lagurus curtatus* (all subspecies) in the unusual, almost heart shaped, median process, and in larger size. *Lagurus luteus* examined by Dearden (1958:545) differs from both *Lagurus lagurus* and *Lagurus curtatus* in lacking lateral digital ossifications and in having shorter median digital ossifications and wider base of stalk.

Specimens examined: Seven *Lagurus curtatus levidensis* from Wyoming; 9 mi. S Robertson, Uinta Co., 26045, 26053; 8 mi. S, 2½ mi. E Robertson, Uinta Co., 26049; Farson, Sweetwater Co., 37906; 16 mi. S, 11 mi. W Waltman, Natrona Co., 42457; 32 mi. S, 22 mi. E Rock Springs, 42465, 42466.

The following key to the bacula in some adult North American Microtinae is intended to help point out some of the most important differences. It should be noted that not all species can be keyed out on the basis of the baculum. The most difficult group in this respect includes the species of *Microtus* that have small or no ossified lateral processes, especially species of the subgenera *Pedomys* and *Pitymys*, and the two species *Microtus californicus* and *Microtus mexicanus* of the subgenus *Microtus*. Another complicating factor is the variability of bacula evident in some species even in the small samples available.

It is to be expected that additional specimens will show variations not yet observed.

KEY TO THE BACULA OF SOME NORTH AMERICAN MICROTINES

1. Length of lateral digital ossifications more than ⅓ breadth of stalk 2
1'. Length of lateral digital ossifications less than ⅓ breadth of stalk or absent 15
2. Size small (total length of baculum less than 5.5 mm.) 3
2'. Size large (total length of baculum more than 5.5 mm.) 14
3. Width at mid-point of stalk more than ⅓ greatest breadth of stalk 4
3'. Width at mid-point of stalk less than ⅓ greatest breadth of stalk, 8
4. Stalk, viewed from proximal end hour-glass shaped, and width of stalk less than ½ length of stalk ..... *Phenacomys intermedius*, p. 197
4'. Stalk not both hour-glass shaped when viewed from proximal end, and with width less than ½ length of stalk 5
5. Shaft thin basally, thickness less than ⅓ of greatest breadth 6
5'. Shaft thick basally, thickness ⅓ or more of greatest breadth 7
6. Stalk more or less straight, base not deflected. *Microtus oeconomus*, p. 204
6'. Stalk spatulate, and base deflected from axis of shaft ..... *Microtus guatemalensis*, p. 198
7. Base enlarged, depth nearly ½ of breadth ... *Lemmus trimucronatus*, p. 193
7'. Base moderately enlarged, depth near ⅓ of breadth ..... *Microtus pennsylvanicus*, p. 206, or *Microtus townsendii*, p. 204
8. Base hour-glass shaped as viewed from proximal end ..... *Phenacomys intermedius*, p. 197
8'. Not so 9
9. Lateral processes separated from tip of shaft by more than the thickness of the lateral process 10
9'. Lateral processes separated from tip of shaft by less than the thickness of the lateral process 11
10. Lateral processes more than ½ the width of median process ..... *Microtus longicaudus*, p. 201
10'. Lateral processes slender, less than ½ the width of median process ..... *Microtus montanus*, p. 204
11. Lateral ossifications equal in length to median ossification ..... *Clethrionomys*, p. 194
11'. Lateral ossifications shorter than median ossification 12
12. Size small, less than 3.4 mm. in total length .... *Microtus oregoni*, p. 199
12'. Size medium, more than 3.4 mm. in total length 13
13. Greatest width of stalk at a point about ⅓ of length of stalk from base ..... *Microtus chrotorrhinus* (Hamilton, 1946:382).
13'. Greatest width of stalk at a point less than ⅓ of length of stalk from base ..... *Lagurus curtatus*, p. 210
14. Size of baculum larger, base more than 3 mm. wide, processes all well developed ..... *Ondatra zibethicus*, p. 198
14'. Size of baculum smaller, base less than 3 mm. wide, processes poorly developed in some animals ..... *Neofiber alleni*, p. 209
15. At least one digital ossification present 16

15'. Digital ossifications not present ..... *Dicrostonyx groenlandicus*, p. 193
16. Breadth of stalk at least ½ length of stalk 17
16'. Breadth of stalk less than ½ length of stalk 19
17. Length of stalk greater than 3.6 mm. and less than 1½ times its greatest breadth ..... *Microtus richardsoni*, p. 199
17'. Length of stalk usually less than 3.6 mm., or if more than 3.6 mm. (up to 4.0 mm.) then length 1½ times or more its greatest breadth 18
18. Median process attenuate distally in dorsal view, and relatively long (more than twice its own breadth), ⅕ to ⅗ the length of stalk; breadth of stalk usually ⅔ or more length of stalk ..... *Microtus miurus*, p. 200
18'. Median process relatively blunt distally in dorsal view, relatively short (usually less than ¼ length of stalk), breadth of stalk usually less than ⅔ length of stalk ..... *Pitymys*, p. 208, *Pedomys*, p. 207, or *Microtus mexicanus*, p. 205
19. Distal processes small and firmly ankylosed to distal end of shaft ..... *Phenacomys longicaudus*, p. 197
19'. Distal processes if present not firmly ankylosed to distal end of shaft 20
20. Dorsal concavity of base as viewed from proximal end usually deeper than ventral concavity ..... *Microtus mexicanus*, p. 205
20'. Dorsal and ventral concavities of base equal in depth or ventral one the deeper 21
21. Total length of baculum more than 3.6 mm. ..... *Microtus californicus*, p. 205
21'. Total length of baculum less than 3.6 mm. ..... *Synaptomys cooperi*, p. 194

DISCUSSION

Owing to shortness of lower incisors and present geographic distribution of the species, Hinton (1926:35) considered the Tribe Lemmi (lemmings) to be more primitive than the Tribe Microti (voles). The surviving lemmings are specialized in many features and therefore are considered as advanced end-products of an evolutionary radiation of a primitive microtine stock, of which all earlier stages are extinct.

Hinton regarded *Dicrostonyx* as the most primitive of the genera of lemmings on account of its more complex molar teeth (complexity was considered to be primitive), and on account of the presence of three primitive longitudinal rows of tubercles in unworn molars. The other three genera were arranged in order of increasing specialization as follows: *Synaptomys, Myopus, Lemmus.*

If the baculum tended to retain its primitive character while specializations in the external anatomy developed, and if the above arrangement is correct the most primitive bacula would be found in *Dicrostonyx* and in *Synaptomys.* The baculum in these two genera in comparison to that in *Myopus* (as figured by Ognev, 1948:

512) and *Lemmus* has a slenderer stalk and smaller digital ossifications or none at all. The baculum in the genera of lemmings increases in robustness and the development of processes from *Dicrostonyx,* to *Synaptomys,* to *Myopus,* to *Lemmus*—the same order outlined above for total of specialization. The two extremes in this series are near the extremes of variation in bacula to be found in all microtines. The baculum in lemmings as a group cannot then be considered more primitive than in voles as a group, although the voles are usually considered to be more advanced. The situation in the voles, as we shall see, casts a different light on the matter.

The voles, Tribe Microti, were considered by Hinton (1926:40) to be more advanced than the lemmings because the incisors of the voles are longer and the root of their last lower molar is lingual to the root of the incisor. Hinton thought also that the murine ancestors of microtines had shorter incisors and that the backward extension of the incisors in the voles is a more ancient feature than the hypsodonty of the molars. A trend in the molar teeth has been toward greater hypsodonty. The voles in which the molars are least hypsodont are thus considered primitive. These include the living genera *Clethrionomys, Phenacomys, Ondatra, Dolomys, Ellobius,* and *Prometheomys.* Therefore, the baculum, in these assumedly primitive genera, would be expected to resemble the baculum in the lemmings or at least the most primitive lemmings. This is not the case.

The bacula that I have examined of *Clethrionomys* and *Phenacomys* have well-developed digital ossifications. In this they resemble the baculum of the genus *Lemmus,* the most advanced genus of lemmings according to Hinton. The baculum of *Dolomys* has not been studied. The baculum in *Ondatra,* and in *Prometheomys* as illustrated by Ognev (1948:552), also possesses well-developed processes. The baculum of *Ellobius* is small and lacks processes (as figured by Ognev, 1950:662). No ossification was found in a single specimen of *Ellobius* examined by me although the entire glans penis was removed and cleared without dissection. So far as known then, with the exception of *Ellobius* and *Phenacomys longicaudus* (Dearden, 1958:547), the primitive microtines having rooted molars possess bacula having three well-developed ossified processes.

Voles of the genus *Microtus* vary in the structure of the baculum almost as much as do the lemmings. Within the single subgenus *Microtus* some individuals of *Microtus mexicanus,* for example, have minute ossified lateral processes and other individuals lack these

processes; *Microtus pennsylvanicus* and some other species have proportionately large lateral ossifications. If the well-developed condition of the baculum in the microtines having rooted molars is primitive, then within the genus *Microtus* those species having well-developed bacula may be considered primitive.

The genera *Lagurus* and *Neofiber* have moderately developed or well-developed lateral processes. *Neofiber* exhibits a tendency, not prominent elsewhere, to have a proportionately smaller median process rather than reduced lateral processes.

American species of *Microtus* (genus and subgenus) that have moderately- to well-developed ossified lateral processes are *M. townsendii, M. oeconomus, M. pennsylvanicus, M. montanus,* and *M. chrotorrhinus. Microtus* of other subgenera having this type of baculum include *M.* (*Herpetomys*) *guatemalensis, M.* (*Chilotus*) *oregoni,* and *M.* (*Chionomys*) *longicaudus.*

American species of *Microtus* (genus and subgenus) in which the lateral ossifications are weakly developed or absent (although cartilaginous lateral processes are present) include *M. mexicanus* and *M. californicus.* In other subgenera, species of *Microtus* having reduced lateral ossifications are *M.* (*Pedomys*) *ochrogaster, M.* (*Pitymys*) *pinetorum, M.* (*Pitymys*) *parvulus, M.* (*Pitymys*) *quasiater, M.* (*Arvicola*) *richardsoni,* and *M.* (*Stenocranius*) *miurus.*

The microtines are essentially holarctic in distribution. Both of the tribes, the lemmings and the voles, as well as primitive representatives of each tribe (not considering *Ellobius*) occur in both the Old World and New World. It is not certain on which continent (or continents) the Microtinae first differentiated. It is certain, however, that at various times, both early and late in the evolution of the subfamily, representatives have crossed from Eurasia to North America or *vice versa.* Each of 10 or more microtines in the New World is more closely related to some microtine in the Old World than to any other microtine in the New World.

The similarities or differences in the baculum in Old World and New World representatives placed in the same genus or subgenus, or thought to be "companion species" have been commented upon in accounts of *Lemmus, Dicrostonyx, Clethrionomys, Lagurus, Arvicola, Stenocranius, Chilotus, Chionomys, Pitymys,* and in accounts of *Microtus agrestis* as compared with *M. pennsylvanicus,* and *Microtus oeconomus* (both Old World and New World).

The baculum in the Microtinae more closely resembles the baculum in the Cricetinae of the Old World than in the Murinae, or than in any other rodents known to me. This resemblance suggests relationship between Microtinae and Cricetinae.

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A New Order of Fishlike Amphibia From the Pennsylvanian of Kansas

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INTRODUCTION

A slab of shale obtained in 1955 by Mr. Russell R. Camp from a Pennsylvanian lagoon-deposit in Anderson County, Kansas, has yielded in the laboratory a skeleton of the small amphibian *Hesperoherpeton garnettense* Peabody (1958). This skeleton provides new and surprising information not available from the holotype, No. 9976 K. U., which consisted only of a scapulocoracoid, neural arch, and rib fragment. The new specimen, No. 10295 K. U., is of the same size and stage of development as the holotype and it is thought that both individuals are adults.

The quarry, University of Kansas Museum of Natural History Locality KAN 1/D, is approximately six miles northwest of Garnett, Anderson County, Kansas, in Sec. 5, T. 19S, R. 19E, 200 yards southwest of the place where *Petrolacosaurus kansensis* Lane was obtained (see Peabody, 1952). The Rock Lake shale, deposited under alternately marine and freshwater lagoon conditions, is a thin member of the Stanton limestone formation, Lansing group, Missourian series, and thus is in the lower part of the Upper Pennsylvanian.

Peabody (1958) placed *Hesperoherpeton* in the order Anthracosauria, suborder Embolomeri, family Cricotidae. Study of the second and more complete specimen reveals that *Hesperoherpeton* is unlike the known Embolomeri in many important features. The limbs and braincase are more primitive than those so far described in any amphibian. The vertebrae are comparable to those of Ichthyostegalia (Jarvik, 1952), as well as to those of Embolomeri. The forelimb is transitional between the pectoral fin of Rhipidistia and the limb of early Amphibia. The pattern of the bones of the forelimb closely resembles, but is simpler than, that of the hypothetical transitional type suggested by Eaton (1951). The foot seemingly had only four short digits. The hind limb is not known.

The new skeleton of *Hesperoherpeton* lies in an oblong block of limy shale measuring approximately 100 x 60 mm. After preparation of the entire lower surface, the exposed bones and matrix were embedded in Bioplastic, in a layer thin enough for visibility

but giving firm support. Then the specimen was inverted and the matrix removed from the opposite side; this has not been covered with Bioplastic. The bones lie in great disorder, except that some parts of the roof of the skull are associated, and the middle section of the vertebral column is approximately in place. The bones of the left forelimb are close together but not in a natural position. The tail, pelvis, hind limbs and right forelimb are missing. Nearly all the bones present are broken, distorted by crushing, incomplete and scattered out of place, probably by the action of currents. The complete skeleton, in life, probably measured between 150 and 200 mm. in length.

The specimen was studied at the Museum of Natural History, University of Kansas, with the help of a grant from the National Science Foundation, number NSF-G8624. The specimen was discovered in the slab by Miss Sharon K. Moriarty, and was further cleaned by the authors. Mr. Merton C. Bowman assisted with the illustrations. We are indebted to Dr. Robert W. Wilson for critical comments.

SKULL

Dorsal Aspect (Figs. 1, 2)

In reconstruction, the skull measures approximately 8.0 mm. dorsoventrally at the posterior end. The height diminishes anteriorly to about 1.5 mm. at the premaxillary. The length is about 15.5 mm. in the median line, or 24.0 mm. to the tip of the tabular, and the width about 16.0 mm. posteriorly. The snout is blunt, continuing about 1-2 mm. anterior to the external nares. Each of the tabulars has a slender posterior process 5.0 mm. long, which probably met the supracleithrum; the intertabular space is about 8.5 mm. wide. The orbits are approximately 5.5 mm. in diameter and extend from the maxillary to within about 3.0 mm. of the midline dorsally. The pineal opening is 1.8 mm. anterior to the occipital margin of the skull.

Reduction of bones at the back of the skull seems to have eliminated any dermal elements posterior to the squamosal, while enlargement of the orbit has removed most of the postorbital series, leaving the squamosal as the only cheekbone. There is apparently no jugal or postfrontal.

The squamosal of *Acanthostega* (Jarvik, 1952) is articulated under the tabular and reaches forward and down, much as if it were an opercular in reversed position. Internally, it must lie against the otic capsule below the tabular, partially concealing the stapes.

The bone that we suppose to be the squamosal of *H. garnettense* is of similar shape, of about the same size and has internally an articular surface at one corner, bounded by a pair of ridges in the shape of a V. This articular surface probably fitted on a lateral process extending from the roof of the neurocranium, over the front of the otic capsule.

The premaxillary extends posterolaterally to a distance 5.5 mm. from the midline and attains a width at its broadest point of about 1.5 mm. The posterior edge is slightly concave and in part forms the anterior border of the naris.

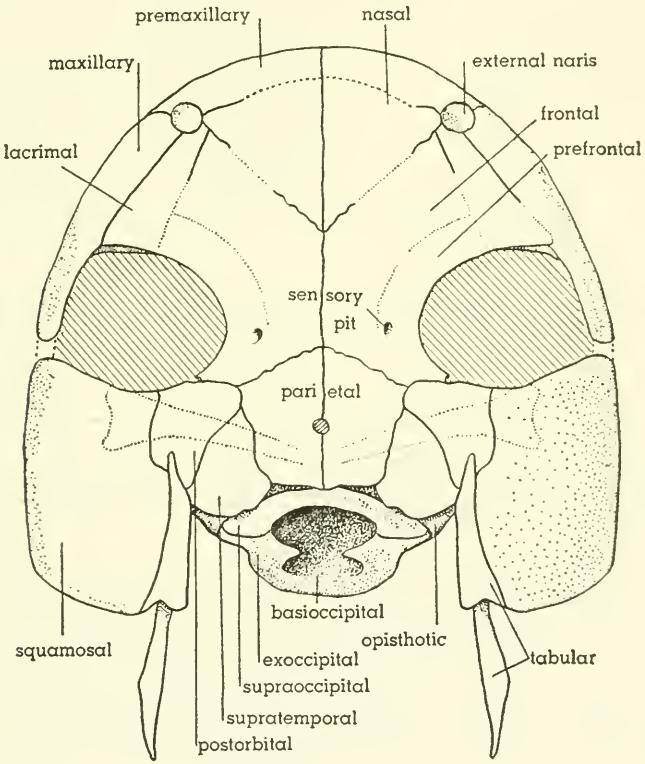

Fig. 1. *Hesperoherpeton garnettense* Peabody. Skull, dorsal view. Postorbital processes of the neurocranium are shown in dotted outline. KU 10295, × 4.

The nasal is triangular and, with the lacrimal, forms the medial border of the naris. The length of the medial side of the nasal bone is approximately 5.0 mm., the transverse width is 3.8 mm., and the extent of the posterolateral border is 5.5 mm.

The maxillary meets the premaxillary lateral to the naris, borders the naris posteroventrally, and continues posteriorly beneath the orbit, of which it forms the external border. The maxillary is about 8.5 mm. long, and immediately anterior to the orbit has a maximum width of 1.3 mm.

The lacrimal fills the remaining rim of the narial opening between the nasal and maxillary, and extends to the anterior edge of the

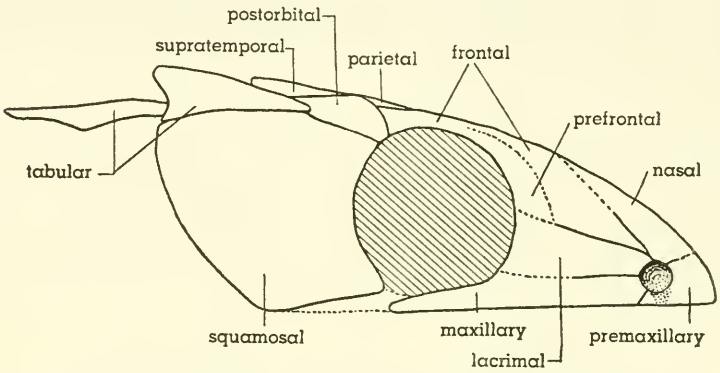

FIG. 2. *Hesperoherpeton garnettense* Peabody. Skull, lateral view, showing relatively large orbit and absence of smaller circumorbital bones. KU 10295, × 4.

orbit. The length, from naris to orbit, is 4.2 mm.; the width ranges from 1.0 mm. anteriorly to 2.5 mm. posteriorly.

The external naris is approximately 1.0 mm. in diameter. It is slightly anterodorsal to the internal naris and 4.0 mm. lateral to the midline.

The dorsal margin of the orbit appears to be formed by the frontal. The anterior part of this margin, however, may be formed by a prefrontal, which is not clearly set off by a suture. The frontal extends 3.8 mm. in the midline, and anteriorly and laterally borders the nasal and lacrimal, respectively. A faint pattern of pitting radiates on the surface from the center of ossification of the frontal. There is also a pit indicating the presence of a supraorbital sensory pore.

The parietal bones enclose the pineal opening, approximately 2.5 mm. posterior to the suture with the frontal. The foramen is about 0.5 mm. in diameter. Laterally the parietal meets the medial angle of the postorbital and the medial border of the supratemporal. No bone of this animal shows the deep pitting and heavy ornamentation characteristic of many primitive Amphibia.

The postorbital meets the anterolateral corner of the parietal for a distance of 0.5 mm., the anterior edge bordering the frontal bone and the orbit for a combined distance of about 3.0 mm. The lateral margin is slightly convex, and is probably interrupted behind by the anterior point of the tabular. Medially, the concave margin of the postorbital meets the supratemporal for about 3.5 mm.

The supratemporal is thus wedge-shaped and located between the parietal and the postorbital. The posterior edge of the supratemporal protrudes as a convex border slightly behind the end of the parietal, and measures 3.0 mm. around the curve to the parietal suture.

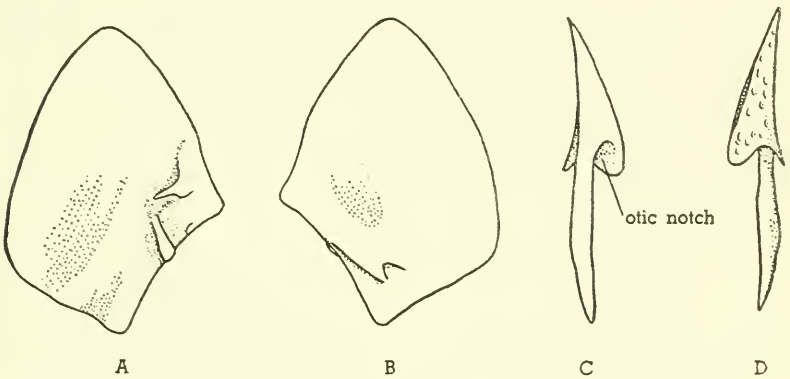

Fig. 3. *Hesperoherpeton garnettense* Peabody. A, left squamosal, internal surface. B, left squamosal, external surface. C, right tabular internal surface. D, right tabular, external surface. KU 10295, all × 4.

The squamosal (Fig. 3 A, B) is a large, somewhat rectangular bone extending from the back of the orbit to the posterior extremity of the cheek. It outlines almost entirely the posterior border of the orbit, the ventrolateral portion of the cheek region, and the lateral border of the top of the skull behind the orbit. Dorsally, the squamosal meets the anterior half of the tabular and the lateral border of the supratemporal. Near the anteroventral edge of the squamosal there is a small pit, probably related to a postorbital sensory pore in the skin.

The tabular (Fig. 3 C, D) is pointed anteriorly, where it probably fits against the lateroposterior edge of the postorbital. The dorsal part of the bone flares out and down, forming a small otic notch at a point halfway back. Posteriorly, the flange attains a dorsoventral width of 2.0 mm. at the edge of the notch. The slender posterior

process of the tabular which continues beyond the flange is approximately 0.5 mm. in diameter and 5.0 mm. long.

Ventral Aspect (Fig. 4)

The palatal view of the skull shows the paired premaxillary, maxillary, palatine, pterygoid, and quadrate bones. The openings for the internal nares, the ventral orbital fenestrae, and the subtemporal fossae are readily recognized. The quadrate processes extend posteriorly leaving a large gap medially at the posterior end of the skull.

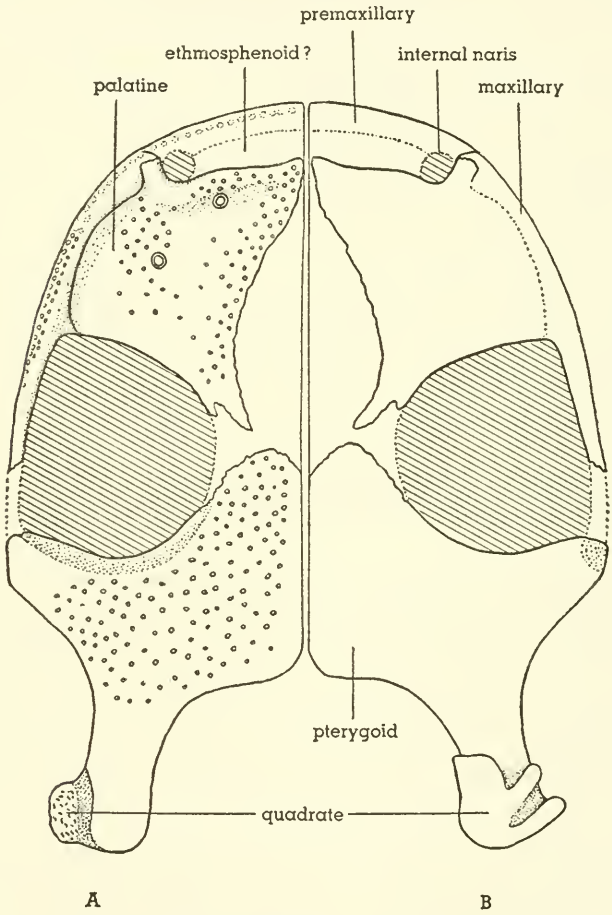

FIG. 4. *Hesperoherpeton garnettense* Peabody. Palate reconstructed; ventral aspect at left, showing teeth, dorsal aspect at right. KU 10295, × 4.

The left quadrate appears to be in place on the posterior prong of the pterygoid. The dorsal side of the quadrate is grooved between two anterolaterally directed ridges. The groove, which probably held the end of the stapes, extends about half the width of the quadrate itself. The width of the quadrate is 4.0 mm., the length is 4.5 mm. medially and about 2.0 mm. laterally. In ventral view the quadrate appears to project laterally, but is incomplete and its shape uncertain. The distance from the posterior end of the quadrate to the visible posterior edge of the orbital fenestra, which opens ventrally, is 10.0 mm.

This region between the quadrate and the orbit is occupied by a pterygoid with three projections. Anteriorly, the pterygoid outlines most of the posterior edge of the orbit (a distance of about 6.5 mm.). A lateral process separates the orbit from the subtemporal fossa. A posteriorly directed edge defines the fossa, which extends about 6.5 mm. anteroposteriorly. The lateral process of the pterygoid terminates 10.0 mm. from the midline. Both the lateral and posterior pterygoid processes are approximately 2.0 mm. wide. The greatest width of the subtemporal fossa is about 2.0 mm. The medial border of the orbital fenestra is missing, but apparently consisted of the pterygoid for at least the posterior half.

Along the posterior edge of the orbital fenestra, there is a narrow, dorsally projecting flange of the pterygoid. The lateral opening of the orbit is approximately 7.5 mm. wide.

The remaining border of the orbital fenestra on the anterior and medial sides is formed by a bone occupying the position of palatine and vomer; for convenience we designate this as palatine. When reconstructed in its probable position in relation to the pterygoid, the left palatine lacks a section, on its medial and posterior edges, measuring about 2.5 mm. by 9.0 mm. The lateral margin of the palatine is convex; about 5.5 mm. anterior to the orbit this margin curves into a strong anteriorly pointing projection, medial to which is seen the internal narial opening. The remaining anterior edge is slightly convex, smoothly rounded, and meets the midline about 9.0 mm. anterior to the pterygoid.

The void area medial to the palatine and anterior to the pterygoid does not fit any bone which we can recognize as the parasphenoid. It is thus suspected that this area is covered in part by the missing edge of the palatine and partly by an anteromedial extension of the pterygoid. Of course a parasphenoid may also have been present.

The position, length, and shape of the premaxillary shown in palatal view (Fig. 4) are primarily based upon the dorsal appearance since ventrally most of it cannot be seen. At the point where it forms the anterior border of the internal naris, the premaxillary is slightly wider than the maxillary and seems to become narrower as it approaches the midline.

The ethmosphenoid, which we cannot identify, may have been exposed in a gap between the premaxillary and the palatine. The gap measures approximately 8.0 mm. wide and ranges up to 1.0 mm. anteroposteriorly.

The maxillary begins at a suture with the premaxillary lateral to the naris and continues posteriorly, bordering the orbit with a width of about 1.2 mm. It then tapers to a point approximately 2.0 mm. anterior to the lateral projection of the pterygoid. The width of the maxillary at this point is 0.8 mm. and the posterior end is broken; probably when complete it approached the pterygoid, and either met the latter or had a ligamentous connection with it. As nearly as can be determined, the total length of the maxillary is approximately 12.0 mm.

The teeth on the maxillary are small and seem to be in two longitudinal rows. The palatine bears two large, grooved teeth anteriorly; the first is approximately 1.0 mm. posteromedial to the naris and the second is about 3.0 mm. posterior and slightly lateral to the naris. The flat ventral surfaces of the palatine and pterygoid bear numerous small teeth distributed as shown in Fig. 4.

Braincase and Occipital Region (Fig. 5)

The parts of the neurocranium are scattered, disconnected and incomplete, but it is possible to make out a number of features of the otico-occipital section with fair assurance. In posterior view the notochordal canal and foramen magnum are confluent with each other, and of great size relative to the skull as a whole. The notochordal canal measures 2.8 mm. in diameter, and the foramen magnum about 4.0 mm. The crescent-shaped supraoccipital rests on the upright ends of the exoccipitals, but between the latter and the basioccipital no sutures can be seen. Probably the whole posterior surface of the braincase slanted posteroventrally; consequently the rim of the notochordal canal was about 3.0 mm. behind the margin of the parietals.

The U-shaped border of the notochordal canal is a thick, rounded bone, comparable in appearance to the U-shaped intercentra of the

vertebrae. This bone apparently rested upon a thinner, troughlike piece (Fig. 5 B) forming the floor of the braincase. The latter is broad, shallow, concave, open midventrally and narrowing anteriorly to form a pair of articular processes. Since no sutures can be seen in this structure, it probably is the ventral, ossified portion of the basioccipital. Watson (1926, Fig. 4 B) illustrates the floor of the braincase in *Eusthenopteron,* with its more lateral, anterior portion labelled prootic, but in our specimen the corresponding part could scarcely have formed the anterior wall of the otic capsule,

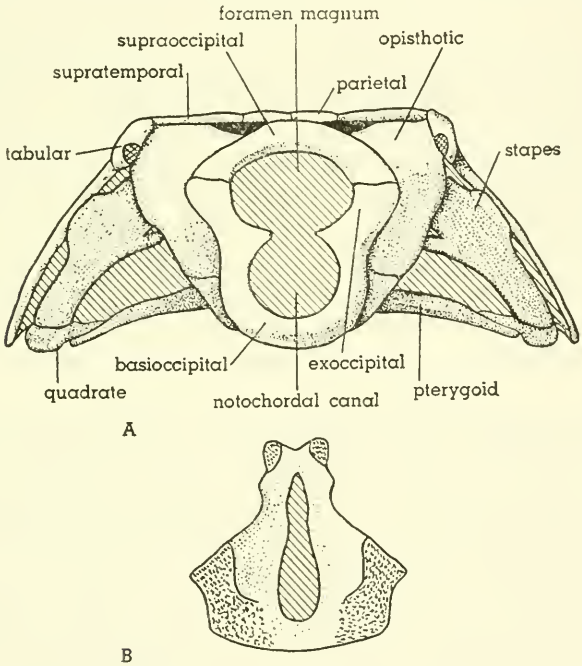

Fig. 5. *Hesperoherpeton garnettense* Peabody, KU 10295, × 4. A, occipital view of skull; B, basioccipital bone in dorsal (internal) view.

being entirely in the plane of the floor. The two articular surfaces anteriorly near the midline suggest that a movable joint existed between the otico-occipital part of the braincase and the ethmosphenoid part, as in Rhipidistia (Romer, 1937). We have found nothing in the specimen that could be referred to the ethmosphenoid; it may have been unossified.

The otic capsules appear to have rested against lateral projections of the basioccipital. The single otic capsule that can be seen (the

right) is massively built, apparently ossified in one piece, with a shallow dorsomedial excavation, probably the vestige of a supratemporal fossa. On the lateral face is a broad, shallow depression dorsally, and a narrower, deeper one anteroventrally; these we suppose to have received the broader and narrower heads of the stapes, respectively. The posterior wall of the otic capsule we have designated opisthotic in the figure. Anterior to the otic capsule the lateral wall of the braincase cannot be seen, and may not have been ossified.

The roof of the braincase is visible in its ventral aspect, extending from approximately the occipital margin to a broken edge in front of the parietal foramen, and laterally to paired processes which overlie the otic capsules directly behind the orbits (see dotted outlines in Fig. 1). Each of these postorbital processes, seen from beneath, appears to be the lateral extension of a shallow groove beginning near the midline. Presumably this section of the roof is an ossification of the synotic tectum. It should be noted that the roof of the braincase proper is perfectly distinct from the overlying series of dermal bones, and that the parietal foramen can be seen in both. The roof of the braincase in our specimen seems to have been detached from the underlying otic capsules and the occipital wall.

The bone that we take to be the stapes is blunt, flattened (perhaps by crushing), 5.0 mm. in length, and has two unequal heads; its width across both of these is 4.0 mm. The length is appropriate to fit between the lateral face of the otic capsule and the dorsal edge of the quadrate; the wider head rests on a posterodorsal concavity on the otic capsule, and the smaller fits a lower, more anterior pit. Laterally the stapes carries a short, broad process that probably made contact with a dorsally placed tympanic membrane. Thus the bone was a hyomandibular in the sense that it articulated with the quadrate, but it may also have served as a stapes in sound-transmission. It contains no visible canal or foramen.

Mandible (Fig. 6)

The crushed inner surface of the posterior part of the left mandible and most of the external surface of the right mandible are preserved in close proximity. Although the whole length of the tooth-bearing margins is missing, some parts of six elements of the right mandible can be seen. The pattern of sutures and the general contour closely resemble those of *Megalichthys* (Watson, 1926, Figs. 37, 38) and other known Rhipidistia.

The anteroposterior length of the mandible is about 23.8 mm., and the depth is 3.8 mm. The dentary extends approximately 17.6 mm. back from the symphysis, and its greatest width is probably 2.0 mm. Its lower edge meets all the other lateral bones of the jaw. The splenial and postsplenial form the curved anteroventral half of the jaw for a distance of about 9.0 mm. The fragmented articular, on the posterior end of the jaw, is 4.0 mm. long and 2.0 mm. deep, exhibiting a broken upper edge; presumably the surface for articulation with the quadrate was a shallow concavity, above the end of the articular.

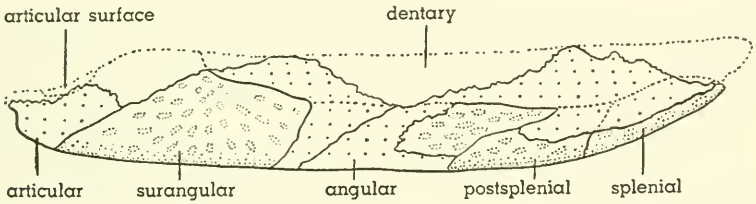

Fig. 6. *Hesperoherpeton garnettense* Peabody. Right mandible, lateral view, KU 10295, × 4. External surfaces are pitted; broken surfaces are coarsely stippled.

VERTEBRAE (Fig. 7)

The vertebrae that are visible from a lateral view are crushed and difficult to interpret. It is possible, nevertheless, to see that the trunk vertebrae resemble those of Ichthyostegalia (Jarvik, 1952, Fig. 13 A, B), except that the pleurocentra are much larger. A few parts of additional vertebrae can be seen, but they are so scattered that it is impossible to be sure of their original location. Therefore comparisons between different regions cannot yet be made.

The U-shaped intercentrum encloses the notochord and occupies an anteroventral position in the vertebra. Anteriorly, each intercentrum articulates with the pleurocentra of the next preceding vertebra by slightly concave surfaces. Dorsolaterally there is an articular surface for the capitulum of the rib.

The two pleurocentra of each vertebra are separate ventrally as well as dorsally, but form thin, broad plates of about the same height as the notochord. The lateral surface appears to be depressed, allowing, perhaps, for movement of the rib. Above each pleurocentrum, on the lateral surface of the neural arch, there is a short diapophysis for articulation with the tuberculum of the rib.

The margin of the neural spine is convex anteriorly and concave posteriorly, the tip reaching a point vertically above the postzyga-

pophysis. The prezygapophysis of each vertebra articulates with the preceding postzygapophysis by a smooth dorsal surface. One nearly complete neural arch shows (Fig. 7 B) a pit above the neural canal, clearly corresponding to the canal for a dorsal ligament shown by Jarvik in *Ichthyostega.* Indeed this view of the neural arch and intercentrum together brings out the striking resemblance between the vertebrae of *Hesperoherpeton* and those of the Ichthyostegids. The rounded intercentrum in both is an incomplete ring enclosing the notochordal canal.

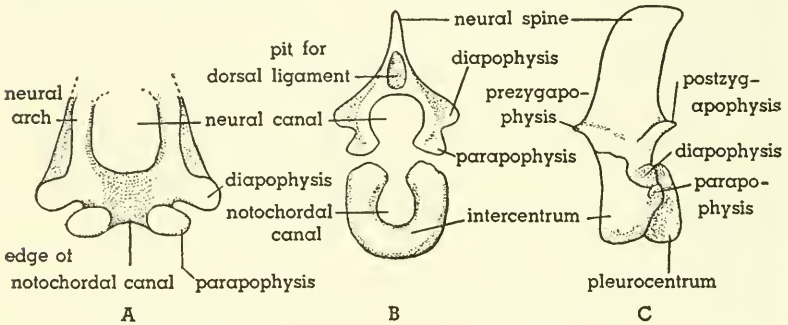

FIG. 7. *Hesperoherpeton garnettense* Peabody. A, End view of incomplete vertebra, probably near anterior end of column. B, Neural arch and intercentrum in end view, showing probable association. C, Left lateral view of trunk vertebra. All figures: KU 10295, ×4.

The shape, in end view, of a partly preserved neural arch (Fig. 7 A) seems to account for the incompleteness of the intercentrum just mentioned; the ventral edge of the arch is emarginate in such a way as to fit the dorsal surface of the notochord. The dorsal portion of this neural arch is not present (either broken or not yet

TABLE 1.—AVERAGE MEASUREMENTS OF THE TRUNK VERTEBRAE (in mm.). NUMBERS IN PARENTHESES INDICATE THE NUMBER OF PIECES AVAILABLE FOR MEASURING

PARTS	Ant.-post.	Dors.-vent.	Transv. width
Neural spine	1.5 (3)	3.0 (3)	.....
Neural spine and arch	2.0 (4)	4.5? (4)	.....
Neural canal	2.0 (4)	2.0 (1)	1.0 (1)
Intercentrum	1.5 (5)	3.5 (4)	3.0 (1)
Pleurocentrum	1.5 (3)	3.0 (2)	.....

ossified), but the opening of the neural canal is comparable in width to the foramen magnum. Hence this vertebra may be one of the most anterior in the column. In comparison with the trunk vertebrae seen farther posteriorly it appears that there may be a progressive ossification of neural arches toward their dorsal ends, and of intercentra around the notochord, with probable fusion of the intercentra and neural arches in the posterior part of the trunk. The notochord seems to have been slightly constricted by the intercentra, but not interrupted.

RIBS

The proximal ends of the ribs expand dorsoventrally to a width approximately four times that of their slender shafts. The tuberculum and capitulum on each of the trunk ribs are separated only by a shallow concavity. These two articular surfaces are so situated that the rib must tilt downward from the horizontal plane. The shaft flares terminally in some ribs, and the distal end is convex. Ribs in the trunk region differ little if any in size. Five that can be measured vary in length from 5.0 to 7.0 mm. One short, bent rib 3.5 mm. long perhaps is sacral or caudal.

PECTORAL GIRDLE (Figs. 8, 9, 10)

The right scapulocoracoid is almost complete, and the left one is present but partly broken into three pieces, somewhat pushed out of position. With the advantage of this new material, we may comment on the scapulocoracoid of *H. garnettense* as described by Peabody (1958). In size and contour, the slight differences between the type (KU 9976) and the new skeleton (KU 10295) are considered to be no more than individual variation. We have redrawn the type (Fig. 8) in order to show the resemblances more clearly.

The small sections that were missing from the type are present in KU 10295. The jagged edge directly posterior to the area occupied by the neural arch in the type extends 0.5 mm. farther back in our specimen. The angle formed between the recurved dorsal ramus and the edge of the ventral flange is seen in our specimen to be less than 90°. The glenoid fossa, appearing as a concave articular surface for the cap of the humerus, was in part covered by cartilage and shows as "unfinished" bone (Peabody, 1958, p. 572); this area is more oval than triangular, as Peabody thought. The obstruction of a clear view of this part of the type is the result of the accidental position of a neural arch. The raised portion

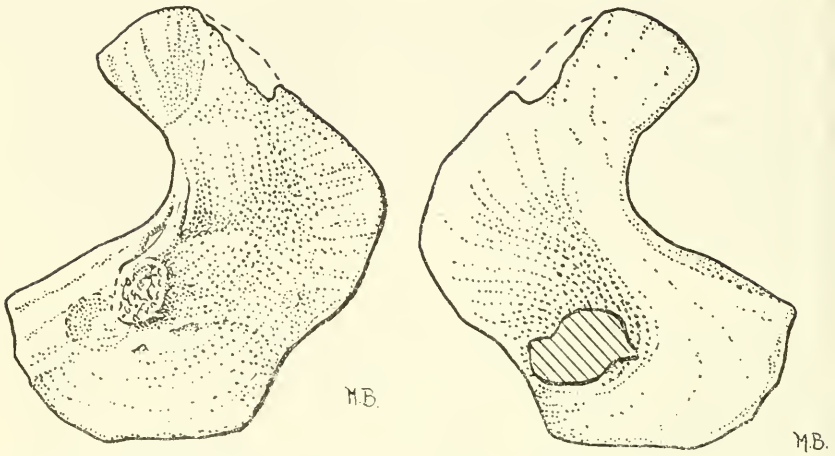

FIG. 8. *Hesperoherpeton garnettense* Peabody. Type specimen redrawn. Right scapulocoracoid in external view (at left), and internal view (at right). KU 9976, × 4.

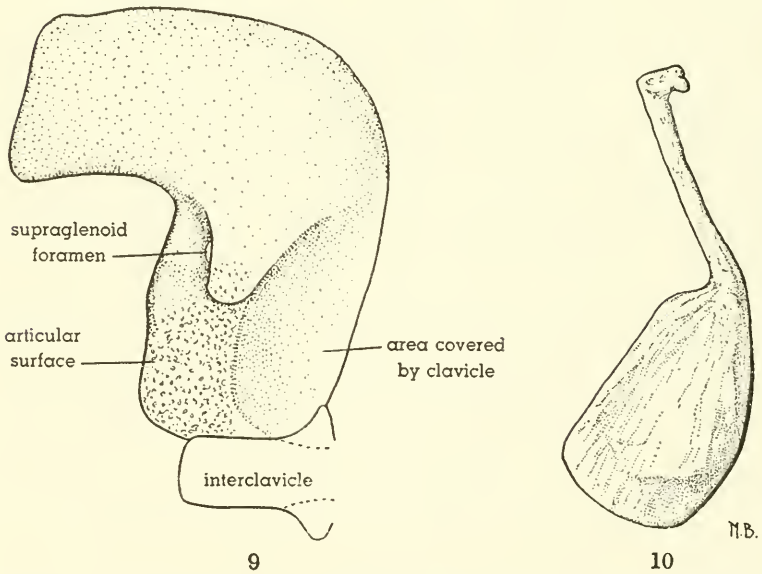

FIG. 9. *Hesperoherpeton garnettense* Peabody. Right scapulocoracoid in external view, showing part of interclavicle, and position occupied by clavicle. The specimen is flattened and lies entirely in one plane. KU 10295, × 4.

FIG. 10. *Hesperoherpeton garnettense* Peabody. Right clavicle in external view. Anterior edge to right. KU 10295, × 4.

immediately dorsal to the glenoid fossa exhibits an unfinished surface, suggesting the presence of either cartilage or a ligament.

The right clavicle is complete, and resembles a spoon having a slender handle. The dorsal tip of the handle is L-shaped. The expanded ventral part is convex externally, and rested upon the anteroventral surface of the scapulocoracoid. The lateral edge next to the "stem" is distinctly concave, abruptly becoming similar in contour to the opposite edge, and giving the impression of an unsymmetrical spoon. The left clavicle is present in scattered fragments, its dorsal hooklike end being intact.

The posterior end of the interclavicle lies in contact with the right scapulocoracoid. There are short lateral processes at the point where the interclavicle was overlapped by the clavicles, but we cannot be sure of the extent of this bone anteriorly or posteriorly.

The presumed left cleithrum, a long rectangle, is approximately equal in length to the rodlike stem of the clavicle, and is about as wide as the dorsal L-shaped tip of the clavicle. The posterior end of the cleithrum presumably met the tip of the clavicle, while the rest of it was directed anteriorly and a little dorsally. There seems to be a small articular surface near the anterior extremity which suggests the presence of a supracleithrum. The upper border of the cleithrum is slightly convex and the lower concave.

FORELIMB (Fig. 11)

The left forelimb is the only one present and appears to be nearly complete, although the elements are scattered almost at random. The only parts of the forelimb known to be missing are two subterminal and two terminal phalanges, probably of the first and third digits, and the proximal end of the second metacarpal. The smooth and relatively flat surfaces suggest an aquatic rather than terrestrial limb; only the proximal half of the humerus bears any conspicuous ridges or depressions. As we restore the skeleton of the limb, several features are remarkable: The humerus, ulna, and ulnare align themselves as the major axis of the limb, each carrying on its posterior edge a process or flange comparable to those in the axial series of a rhipidistian fin. The remaining elements take positions comparable to the diagonally placed preaxial radials in such a fin. The digits appear to have been short, perhaps with no more than two phalanges. There is only one row of carpals present (the proximal row of other tetrapods). A second and third row would be expected in primitive Amphibia; if they existed in *Hesperoherpeton* they must either have been wholly cartilaginous or washed

away from the specimen. Neither of these alternatives seems at all likely to us in view of the well-ossified condition of the elements that are present, and the occurrence of both the proximal carpals and the metacarpals. The space available for metacarpals probably could not have contained more than the four that are recognized.

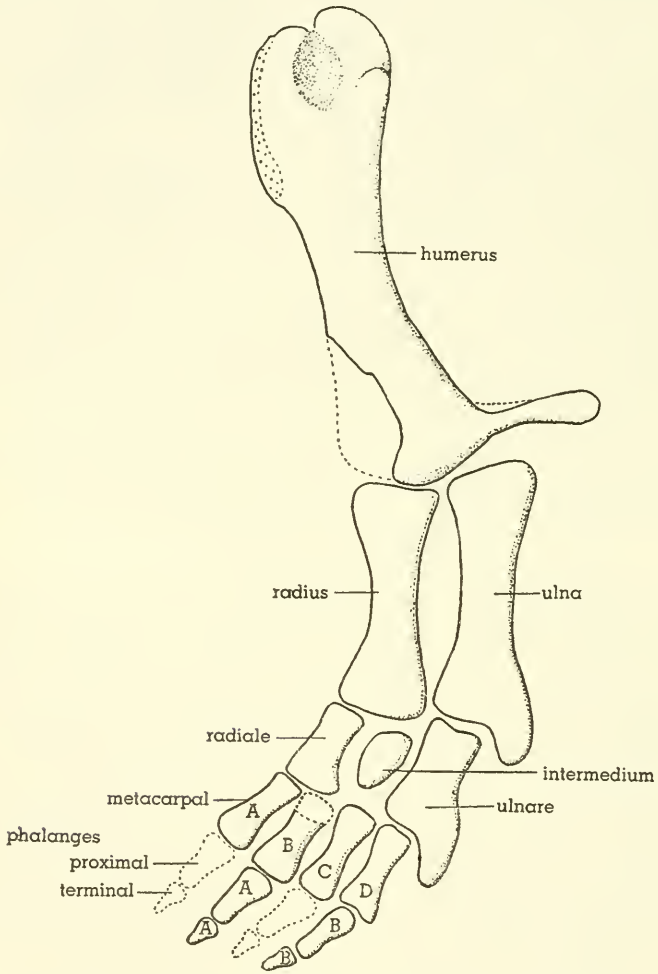

FIG. 11. *Hesperoherpeton garnettense* Peabody. Left forelimb, showing characters of both a crossopterygian fin and an amphibian foot. KU 10295, × 4.

The proximal end of the humerus is more rounded anteriorly than posteriorly, and has a thin articular border that bore a car-

tilaginous cap as the primary surface for articulation with the scapulocoracoid. Although the unfinished surface of the head extends down the anterior margin about a third the length of the humerus, the shaft has been broken and so twisted that the distal part is not in the same plane as the proximal. Immediately posterior to the cartilaginous cap is a round, deep notch bordered posteriorly by the dorsal process of the head.

The shaft is longer and narrower than would be anticipated in a primitive amphibian limb (cf. Romer, 1947). The distal end bears two surfaces for articulation with the radius and ulna. The full extent of the former surface was not determined because the more anterior part of the expanded end is represented only by an impression. The surface nearest the ulna was partially rounded for articulation with that element, the remaining posterior edge being broadly concave. The most striking feature of the humerus is a slender hooklike process on the posterior edge near the distal end, probably homologous with (1) the posterior flange on the "humerus" in Rhipidistia, and (2) the entepicondyle of the humerus in *Archeria* (Romer, 1957) and other tetrapods.

The radius is about the same width proximally as distally. The curvature of the shaft is approximately alike on both sides. Distally the surface is rounded for articulation with the radiale and perhaps the intermedium.

The proximal end of the ulna is similar to that of the radius but is slightly larger. Posteriorly, there is a short, broad expansion resembling the entepicondyle of the humerus, and even more nearly like the postaxial flanges in a crossopterygian fin.

The ends of the radiale are expanded and rounded, the entire bone being approximately twice as long as wide. The three sides of the intermedium are similarly convex. The surface of this bone is unfinished, showing that it must have been embedded in cartilage. The ulnare is conspicuously similar to the ulna in bearing a posterior hooklike expansion, and is larger than the radiale.

The four metacarpals are slightly expanded proximally and distally. Although measurements of length and width are tabulated below (Table 2), we are not certain of the sequence of these bones in the row.

The dimensions of the two proximal phalanges are alike. The shape of these elements is similar to that of the metacarpals. The two terminal phalanges are somewhat triangular in shape, the lateral edges being concave and the proximal convex.

Table 2.—Approximate Measurements of the Forelimb (in mm.)

Element	Dimensions			
	Length	Width		
		Proximal	Midway	Distal
Humerus	16.0	5.0	2.0	7.5?
Radius	9.0	4.0	1.5	3.5
Ulna	8.5	4.5	1.5	3.5
Radiale	3.0	2.0	1.5	2.0
Intermedium	1.5	...	2.0	...
Ulnare	3.5	2.0	2.0	2.5
Metacarpal A	4.5	2.5	1.0	2.0
Metacarpal B	4.5	3.0?	1.5	2.5
Metacarpal C	4.0	2.0	1.5	2.0
Metacarpal D	3.5	2.5	1.0	1.5
Proximal Phalanx A	2.0	1.5	1.0	1.5
Proximal Phalanx B	2.0	1.5	1.0	1.5
Terminal Phalanx A	1.5	1.5	1.0	1.0
Terminal Phalanx B	1.5	1.5	1.0	1.0

COMPARISONS AND DISCUSSION

Apparently primitive rhipidistian characters in *Hesperoherpeton* are: Braincase in two sections, posterior one containing an expanded notochordal canal; lateral series of mandibular bones closely resembling that of *Megalichthys*, as figured by Watson (1926); tabular having long process probably articulating with pectoral girdle; lack of movement between head and trunk correlated with absence of occipital condyle; sensory pits present on frontal and squamosal.

Although we are unable to separate, by sutures, the vomers from the palatines, the palatal surface of these bones and of the pterygoids is studded by numerous small teeth, as in Rhipidistia (Jarvik, 1954) and some of the early Amphibia (Romer, 1947). The stapes apparently reaches the quadrate, and could therefore serve in hyostylic suspension of the upper jaw.

The pectoral limb has an axial series of bones carrying hooklike flanges on their posterior edges. The other bones of the limb show little modification of form beyond the nearly flat, aquatic type seen in Rhipidistia. No distinct elbow or wrist joints are developed.

Characters of *Hesperoherpeton* common to most primitive Amphibia, in contrast with Crossopterygii, are: Nares separated from edge of jaw; stapes having external process that may have met a tympanic membrane, thus giving the bone a sound-transmitting function. Apparently none of the opercular series was present.

There are two large palatal teeth, slightly labyrinthine in character, adjacent to each internal naris. The scapulocoracoid, as shown by Peabody (1958), is Anthracosaurian in structure, as are the long-stemmed clavicles. The limbs have digits rather than fin-lobes, although the digital number apparently is four and the number of bones in the manus is less than would be expected in a primitive amphibian. The vertebrae are similar to those of Ichthyostegids, as described by Jarvik (1952), except that the pleurocentra are much larger.

In addition to this remarkable combination of crossopterygian and amphibian characters, *Hesperoherpeton* is specialized in certain features of the skull. The orbits are much enlarged, probably in correlation with the diminutive size of the animal, and this has been accompanied by loss of several bones. The frontal and squamosal nearly meet each other, and both form part of the rim of the orbit. The bones of the posterior part of the dermal roof are greatly reduced, and there is none behind the squamosal except the projecting tabular; there is no indication of quadratojugal, jugal, intertemporal or postparietal. The foramen magnum is enormous. The external surfaces of the bones of the skull are nearly smooth.

Is it possible that the "primitive" and "specialized" features of this animal are actually larval? Are they not just the kind of characters that would be expected in an immature, aquatic embolomere of Pennsylvanian time? For several reasons we do not think this is the case. Except for the anterior part of the braincase, there is no indication that the skeleton was not well ossified. The postaxial processes on the humerus, ulna and ulnare could scarcely have been larval features only, since they are so clearly homologous with those in adult Rhipidistia; a larval limb should indeed be simple, but its simplicity is unlikely to involve paleotelic adult characters. The scapulocoracoid of our specimen is of practically the same shape and size as that in the only other known individual, the type; this would be probable if both were adults, but somewhat less likely if they were larvae of a much larger animal. The form of the stapes, tabular and otic notch suggest a functional tympanic membrane, which could not have occurred in a gill-breathing larva. On the other hand, an adult animal of pigmy size might be expected to have large orbits, large otic capsules and a large foramen magnum.

We conclude that *Hesperoherpeton* lived and sought food in the weedy shallows at the margin of a pond or lagoon, and that for much of the time its head was partly out of water (Fig. 12). The animal could either steady itself or crawl around by means of the paddle-

like limbs, but these probably could not be used in effective locomotion on land. Like the Ichthyostegids, it probably swam by means of a fishlike tail.

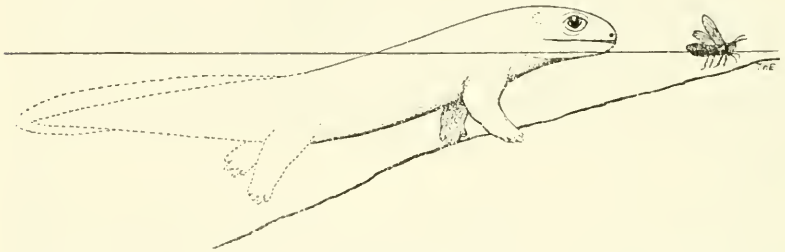

Fig. 12. *Hesperoherpeton garnettense* Peabody. Probable appearance in life. × 0.5.

TAXONOMY

Evidently *Hesperoherpeton* is a small, lagoon-dwelling survivor of the Devonian forms that initiated the change from Crossopterygii to Amphibia (Jarvik, 1955). It shows, however, that this transition did not affect all structures at the same time, for some, as the braincase with its notochordal canal, the mandibular bones and axial limb bones, are unchanged from the condition normal for the Rhipidistia, but most other characters are of amphibian grade. To express these facts taxonomically requires that *Hesperoherpeton* be removed from the family Cricotidae, suborder Embolomeri, order Anthracosauria, and placed in a new order and family of labyrinthodont Amphibia.

Order PLESIOPODA

(*plesios,* Gr., near, almost; *podos,* Gr., foot)

Labyrinthodontia having limbs provided with digits, but retaining posterior flanges on axial bones as in Rhipidistia, without joint-structure at elbow and wrist essential for terrestrial locomotion; neurocranium having separate otico-occipital section, large notochordal canal, no occipital condyle, as in Rhipidistia; nares separate from rim of mouth; pectoral girdle anthracosaurian; vertebrae having U-shaped intercentrum and paired, but large, pleurocentra.

Probably associated with the characters of the order, as given above, are the connection of pectoral girdle with skull, and the presence of a tympanic membrane, the stapes functioning in both sound-transmission and palatoquadrate suspension.

Family HESPEROHERPETONIDAE

Orbits and foramen magnum unusually large in correlation with reduced size of animal; squamosal forming posterior margin of orbit; circumorbital series absent (except for postorbital); sensory pits on squamosal and frontal.

Characters defining the family are evidently the more specialized cranial features, which probably evolved during Mississippian and early Pennsylvanian times.

The definition of the genus and species may be left to rest upon Peabody's (1958) original description and the present account, until the discovery of other members of the family gives reason for making further distinctions.

SUMMARY

Hesperoherpeton garnettense Peabody (1958), based on a scapulocoracoid and part of a vertebra, was originally placed in the order Anthracosauria, suborder Embolomeri, family Cricotidae. A new skeleton from the type locality near Garnett, Kansas (Rock Lake shale, Stanton formation, Upper Pennsylvanian), shows that the animal has the following rhipidistian characters: Large notochordal canal below foramen magnum, otico-occipital block separate from ethmosphenoid, postaxial processes on three axial bones of forelimb, pectoral girdle (probably) articulated with tabular. Nevertheless, *Hesperoherpeton* has short digits, an anthracosaurian type of pectoral girdle, an otic rather than spiracular notch, nostrils separate from the mouth, and vertebrae in which the intercentrum is U-shaped and the pleurocentra large but paired. The stapes reaches the quadrate.

Hesperoherpeton is placed in a new order, PLESIOPODA, on the basis of the characters stated above, and a new family, HESPEROHERPETONIDAE. Specialized characters of the family include: Reduction of circumorbital bones, bringing the squamosal to the edge of the orbit, loss of certain bones of the temporal region, and relative enlargement of the orbits and foramen magnum, in correlation with the diminutive size of the animal. The structural characters of *Hesperoherpeton* suggest to us that it lived in the shallow, weedy margins of lagoons, rested with its head partly out of water, and normally did not walk on land.

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Natural History of the Bell Vireo, Vireo bellii Audubon

BY

JON C. BARLOW

University of Kansas
Lawrence
1962

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JON C. BARLOW

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INTRODUCTION

The Bell Vireo (*Vireo bellii* Aud.) is a summer resident in riparian and second growth situations in the central United States south of North Dakota. In the last two decades this bird has become fairly common in western, and to a lesser extent in central, Indiana and is apparently shifting its breeding range eastward in that state (Mumford, 1952; Nolan, 1960). In northeastern Kansas the species breeds commonly and occurs in most tracts of suitable habitat.

The literature contains several reports dealing exclusively with the Bell Vireo, notably those of Bennett (1917), Nice (1929), Du Bois (1940), Pitelka and Koestner (1942), Hensley (1950) and Mumford (1952). Bent (1950) has summarized the information available on the species through 1943. Nolan (1960) recently completed an extensive report based on a small, banded population at Bloomington, Monroe County, Indiana. He validated for this species many points of natural history previously based on estimates and approximations, especially concerning the post-fledging life of the young and the movement of the adults from one "home range" to another in the course of a single season.

None of these reports, however, has emphasized the ritualized behavioral patterns associated with the maintenance of territory and with courtship. Among the North American Vireonidae, the behavior of the Red-eyed Vireo (*Vireo olivaceus*) is best documented (Sutton, 1949; Lawrence, 1953; Southern, 1958). With this species authors have concentrated on the mechanics of the breeding season and their reports contain little discussion of the aggressive and epigamic behavior of the bird.

The amount of information on the ritualized behavior of the Bell Vireo and related species heretofore has been meager. I observed breeding behavior from its inception in early May through the summer of 1960. It is hoped the resulting information will serve as a basis of comparison in future studies of behavior of vireos; such ethological data are becoming increasingly important, especially as an aid in systematics.

ACKNOWLEDGMENTS

To professors Frank B. Cross, Henry S. Fitch, and Richard F. Johnston of the Department of Zoology of the University of Kansas I am grateful for comments and suggestions in various phases of the study and the preparation of the manuscript. Professor Johnston

also made available data on the breeding of the Bell Vireo from the files of the Kansas Ornithological Society. I am indebted to my wife, Judith Barlow, for many hours of typing and copy reading. Mrs. Lorna Cordonnier prepared the map, Thomas H. Swearingen drew the histograms, and Professor A. B. Leonard photographed and developed the histograms. Dr. Robert M. Mengel contributed the sketch of the Bell Vireo and George P. Young prepared the dummy Bell Vireo used in the field work. Thomas R. Barlow, Donald A. Distler, Abbot S. Gaunt, John L. Lenz, Gary L. Packard, A. Wayne Wiens, and John Wellman assisted in various phases of the field work.

METHODS OF STUDY

Daily observations were made from May 11 to June 26 in 1959 and from April 15 through July 15 in 1960. Six additional visits were made to the study area in September of 1959, and ten others in July and August, 1960. Periods of from one hour to eleven hours were spent in the field each day, and a total of about five hundred hours were logged in the field.

Each territory was visited for at least five minutes each day but more often for twenty minutes. The breeding activities of the pairs were rarely synchronous. Consequently several stages in the cycle of building were simultaneously available for study.

Nine young and one adult were banded in 1959. No Bell Vireos were banded in 1960. Individual pairs could be recognized because of their exclusive use of certain segments of the study area and by the individual variation in the song of the males. Sexes were distinguishable on the basis of differences in vocalizations and plumages.

Most nests were located by the observer searching, watching a pair engaged in building, or following a singing male until the increased tempo of his song indicated proximity to a nest. As the season progressed and the foliage grew more dense, it became increasingly difficult to locate completed nests. Blinds were unnecessary because of the density of vegetation. Observations were facilitated by a 7 x 50 binocular. Data were recorded on the spot in a field notebook. Eggs were numbered by means of Higgins Engrossing ink as they were laid.

Individual trees in which males sang most were marked over a three-week period. Then the distances between the most remote perches were paced. These distances aided in determining the

size of the territories. The general configuration of the vegetation within each territory determined the location of one or more boundaries of the territory. Each territory was given a number, 1, 2, 3, etc., as it was discovered; consequently there is no numerical relationship between the designations of the territories established in 1959 and 1960. Nests within a territory were designated as 1-a, 1-b, 1-c, etc.

Although experimentation was not a primary source of data, it proved useful in certain instances. A stuffed Blue Jay elicited mobbing behavior from nesting pairs. A dummy Bell Vireo elicited both agonistic and epigamic behavior from nesting pairs, depending on the phase of the nesting cycle.

The temperature at the beginning of each day's work was taken by means of a Weston dial thermometer. A hand counter and a pocket watch having a second hand were used in determining such data as frequency of song and periods of attentiveness by the sexes. Histological cross-sections, prepared by A. Wayne Wiens, of the ventral epidermis of both sexes were used to study brood patches.

STUDY AREA

The intensive field work was on a 39-acre tract (fig. 1) extending approximately 7/10 of a mile west from U. S. highway 59, which in 1959-1960 constituted the western city limit of Lawrence, Douglas County, Kansas. The eastern boundary of the study area is approximately 1½ miles southwest of the County Courthouse in Lawrence. The eastern ten acres is associated with the Laboratory of Aquatic Biology of the University of Kansas. The 15 acres adjacent to this on the southwest is owned by the University of Kansas Endowment Association, but is used by Mr. E. H. Chamney for the grazing of cattle. This portion is bounded on the west by a stone fence, beyond which lies a 14-acre field of natural prairie owned by Dr. C. D. Clark that is bordered on the extreme west by a narrow thicket of elm saplings.

The principal topographic feature of the area is an arm of Mount Oread, that rises some 80 feet above the surrounding countryside. About 200 feet from the crest of the southwestern slope of the hill a 40-foot-wide diversion terrace directs run-off toward the two-acre reservoir that is the source of water for eight experimental fish ponds of the laboratory.

The predominant shrub-vegetation consists of Osage orange (*Maclura pomifera*), honey locust (*Gleditsia triacanthos*), and

American elm (*Ulmus americana*). These saplings, ranging in height from 3 to 25 feet, grow in dense thickets as well as singly

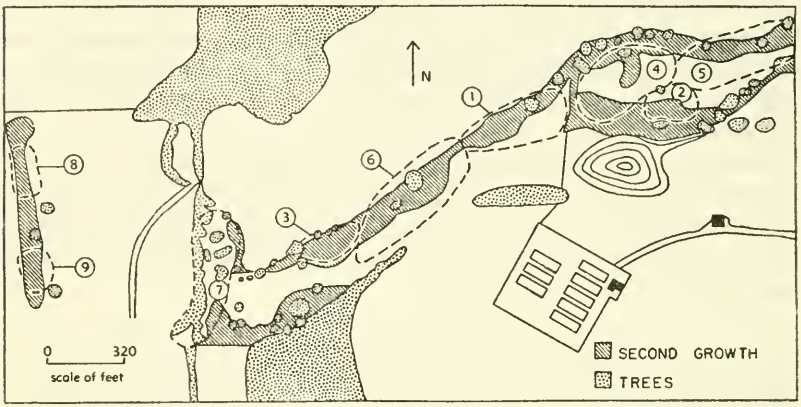

FIG. 1. Map of the study area near the University of Kansas Laboratory of Aquatic Biology. The dashed lines mark the approximate territorial boundaries of the original nine pairs of Bell Vireos from May 1960 to early June 1960.

and in clumps of twos and threes. Larger trees of these same species grow along the crest of the hill, along the eastern and southeastern boundaries of the area, and along the stone fence separating University land from that owned by Dr. Clark. A dense growth of coralberry (*Symphoricarpos orbiculatus*) forms the understory just below the crest of the hill. Isolated clumps of dogwood (*Cornus drummondi*) and hawthorn (*Crataegus mollis*) are scattered throughout the area. These species of shrubs grow densely along the stone fence. The isolated thicket on the Clark land is composed primarily of elm and boxelder (*Acer negundo*), but includes scattered clumps of dogwood, Osage orange, and honey locust. Poplars (*Populus deltoides*) are the only large trees in this area.

The open areas between the thickets are grown up in red top (*Triodia flava*), bluestem (*Andropogon scoparius*), Switchgrass (*Panicum virgatum*), Kentucky bluegrass (*Poa pratensis*), bush clover (*Lespedeza capitata*) and mullen (*Verbascum thapsus*). Shrubby vegetation occupies about 65 per cent of the total area, but in the Clark portion constitutes only about 35 per cent of the ground cover.

Considerations of Habitat

Nolan (1960:226), summarizing the available information on habitat preferences of the Bell Vireo, indicates that this species tolerates "a rather wide range of differences in cover." He pointed

out that a significant factor in habitat selection by this species may be avoidance of the White-eyed Vireo (*V. griseus*) where the two species are sympatric.

In Douglas County where the Bell Vireo is the common species, the White-eyed Vireo reaches the western extent of its known breeding range in Kansas. At the Natural History Reservation of the University of Kansas, where both species breed, the Bell Vireo occurs in "brush thickets in open places" (Fitch, 1958:270) and the White-eyed Vireo occupies "brush thickets, scrubby woodland and woodland edge" (Fitch, *op. cit.*, 268). Along the Missouri River in extreme northeastern Kansas, Linsdale (1928:588-589) found the White-eyed Vireo "at the edge of the timber on the bluff, and in small clearings in the timber," while "the Bell Vireo was characteristic of the growths of willow thickets on newly formed sand bars." Elsewhere in northeastern Kansas I have found the Bell Vireo in shrubbery of varying density and often in habitat indistinguishable from that occupied by White-eyed Vireos at the Natural History Reservation. In the periphery of the region of sympatry the rarer species is confronted with a much higher population density of the common species and consequently might well be limited primarily to habitat less suitable for the common species. This would seem to be the case in eastern Kansas, presuming that interspecific competition exists.

The Bell Vireo has followed the prairie peninsula into Indiana, aided by the development of land for agriculture. In nearby Kentucky where thousands of miles of forest edge are found, and where little brushy habitat of the type preferred by the Bell Vireo occurs, the White-eyed Vireo is abundant whereas the Bell Vireo is unknown as a breeding bird (R. M. Mengel, personal communication).

In more central portions of the area of sympatry, nevertheless, the two species do occur within the same habitat (Ridgway, 1889: 191; Bent, 1950:254) and occasionally within the same thicket (Ridgway, *in* Pitelka and Koestner, 1942:105); their morphological and behavioral differences, although slight, probably minimize interspecific conflict. The Bell Vireo and the Black-capped Vireo (*V. atricapillus*) have been found nesting in the same tree in Oklahoma by Bunker (1910:72); the nest of the black-cap was situated centrally and that of the Bell Vireo peripherally in the tree. Bell Vireos invariably place their nests in the outer portions of trees and peripherally in thickets. This placement would further obviate interspecific conflict with the white-eye since its nests are placed centrally in the denser portions of a thicket.

A critical feature of the habitat preferred by the Bell Vireo is the presence of water. In far western Kansas this species is restricted to riparian growth along the more permanent waterways. This in itself is not adequate proof of the significance of water supply because thicket growth in that part of the state is found only along waterways. The 20 areas over the state that I have visited where Bell Vireos were present were closely associated with at least a semi-permanent source of water. Fifteen other areas indistinguishable from the 20 just mentioned, but lacking a permanent supply of water, also lacked Bell Vireos. Nevertheless areas in which Bell Vireos typically nest are decidedly less mesic than those frequented by White-eyed Vireos.

Once the Bell Vireo was probably more local in its distribution being restricted to thickets associated with permanent water. Clearing of woodland for agricultural and other use, and subsequent encroachment of second growth concomitant with the creation of man-made lakes and ponds, has greatly increased the available habitat for this bird. The preferred species of shrubs for nesting are reported (Bent, 1950:254) to be various wild plums (*Prunus sp.*). The widespread distribution and abundance of the exotic Osage orange has greatly augmented the supply of trees suitable for nesting.

SEASONAL MOVEMENT

Arrival in Spring

The subspecies of the Bell Vireo breeding in Kansas, *V. b. bellii*, winters regularly from Guerrero and the Isthmus of Tehuantepec south to Guatemala, El Salvador, and northern Nicaragua (A. O. U. Check-list, Fifth Edition, 1957:469-470). In the United States migrating birds are first recorded in early March (Cooke, 1909:119). The Bell Vireo is a relatively slow migrator, moving primarily at night and covering little more than 20 miles at a time (Cooke, *op. cit.* 119). The average date of arrival, based on 27 records, for northeastern Kansas is May 8; the earliest record is April 22, 1925, from Manhattan, Riley County, Kansas (fig. 2-A).

In 1959 the first bird arrived at the study tract about May 5. No additional birds were heard singing until the third week of the month, in which eight new males were noted. As mentioned, in 1960 field work was begun in mid-April and the study area was traversed daily. No birds were detected until late afternoon of May 3, when one, presumably a male, was seen foraging.

Lawrence (1953:50) has reported that males of the Red-eyed Vireo precede females in the breeding area by as much as two weeks; the male Red-eyed Vireo forages but sings little in the pre-nesting period. The male Bell Vireo arrives first at the breeding area but precedes the female by only a few days. On the morning of May 4 the first male was singing from a number of perches while ranging over an area of seven acres. This area encompassed terri-

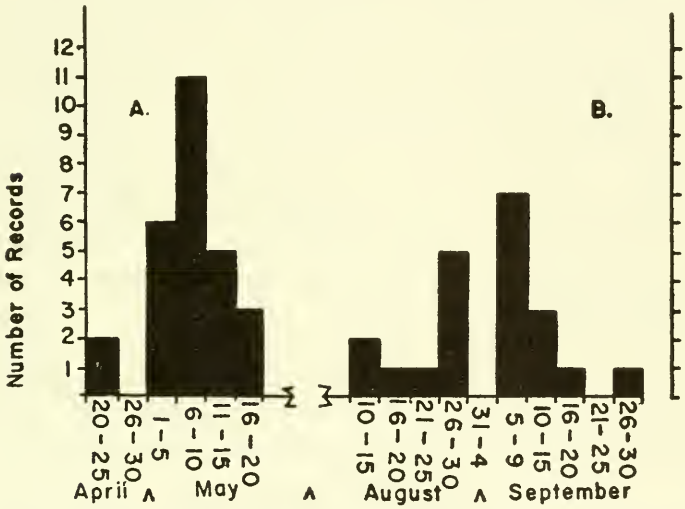

FIG. 2. Seasonal movement as indicated by the curve for spring arrival (A), based on the earliest dates for 27 years, and the curve for autumn departure (B), based on the latest dates for 21 years in northeastern Kansas.

tories later occupied by three pairs, 2 (1960), 4 (1960), and 5 (1960). Late on the afternoon of May 4 the first courtship songs were heard and the first male was seen with a mate at 6:20 p. m. Eight additional males arrived from May 6 through May 18. A tenth male was discovered in the vicinity of territory 9 (1960) on June 18, 1960.

Fall Departure

The average date of departure for 21 years in northeastern Kansas is September 3 (fig. 2-B). The earliest date is August 14 from Concordia, Cloud County, Kansas (Porter, unpublished field notes). The latest date is September 27 (Bent, 1950:262) from Onaga, Pottawatomie County, Kansas. In 1959 the last vireo was seen at the study tract on September 14. The birds do not all depart at the

same time. On September 1 there were still five singing males in the study area; by September 10 there were three and on September 13, only one.

GENERAL BEHAVIOR

Flight

In "straight-away" flight the Bell Vireo undulates slightly. In a typical flight several rapid, but shallow, wing beats precede a fixed-wing glide of from 1 to 15 feet in length. Because the wings are extended horizontally during the glide, the bird does not move distinctly above or below the plane of flight. The White-eyed Vireo generally appears to be slower and more lethargic in flight than the Bell Vireo. In the breeding season most flights of the Bell Vireo are no longer than a few feet between adjacent shrubs and trees, but occasional sustained flights are as long as 300 feet. The birds fly as low as 2 feet above ground, but have often been observed as high as 70 feet above the ground.

In courtship and protracted territorial disputes, where chase between sexual partners or a pair of antagonists occurs, looping flights are observed. The wings are beaten as the birds climb and many aerial maneuvers are performed in the course of the glide.

Foraging and Food Habits

The Bell Vireo has been characterized as a thicket forager (Hamilton, 1958:311; Pitelka and Koestner, 1942:104), but in my experience it is not restricted to low level strata; birds forage from ground level upward, both in thickets and isolated trees ranging in height from 3 feet to 65 feet. The tendency to forage at higher levels is in part dictated by the presence of tall trees within the various territories.

Territories 1 through 7 (1960) contained from three to ten trees surpassing 40 feet in height. They grew singly or in small groves. The Bell Vireos foraged fully 20 per cent of the time in these trees. Food was sought throughout the leaf canopy.

Behavior in foraging in larger trees followed a routine pattern. Typically a pair alighted in a tree at a height of 15 feet. Then the female hopped to a perch a foot above the one upon which she landed. The male succeeded her to the perch she had previously occupied. The pair in effect spiraled around some large, essentially upright, branch, in foraging. The birds usually reached higher

perches in this manner rather than by flying upward 10 to 15 feet to them. This manner of progression within a tree is reminiscent of a similar habit of the *Cyanocitta* jays. Presumably, the habit of the Bell Vireo of foraging in higher strata is facilitated by the absence of other species of arboreal foraging vireos.

Chapin (1925:25) found the Bell Vireo to be more insectivorous in its food habits than any other North American vireo. He found 99.3 per cent of all food contained in 52 stomachs to be of animal origin. Only three times have I seen a Bell Vireo take food of vegetable origin. On September 9, 10, and 14, 1959, I noted a male eating wild cherries over a period of 65 minutes of observation. Chapin (1925:27) noted that beginning in July vegetable matter represented 1.57 per cent of the bird's subsistence, and thereafter slightly more until fall migration.

Animal food, consisting primarily of insects and spiders, is actively sought along branches and under leaves. Often a foraging bird will leap to the underside of a branch and hover, mothlike, beneath a cluster of leaves while extracting some insect. Some individuals hung upside down on small branches, paridlike, while foraging. Lawrence (1953:710), and Southern (1958:201) have recorded similar behavior of the Red-eyed Vireo. Occasionally, I have seen a Bell Vireo fly from a perch and capture an insect in the manner of a flycatcher. The birds do not appear to be adept at this type of food-getting. Nolan (1960:242) mentions Bell Vireos holding hard-bodied insects by means of their feet while breaking the exoskeleton with the beak to obtain the soft parts. Southern (1958: 201) recorded a female Red-eyed Vireo foraging on the ground; I have seen a Bell Vireo on the ground but once, and it was gathering nesting material.

Bathing

On May 14, 1960, in a rill that empties into the northeastern edge of the reservoir a female flew down from a perch six inches above the surface, barely dipped into the water, flew to a perch 12 inches above the water, violently shook her ruffled body feathers, quivered her wings, and rapidly flicked her fanned tail. The entire procedure was repeated three times in five minutes. She was accompanied by a singing male that did not bathe.

Nolan (1960:241) reports a male Bell Vireo bathing by rubbing against leaves wet with dew; he notes that the White-eyed Vireo bathes in a similar manner. Southern (1958:201) twice observed

Red-eyed Vireos bathing in water that dropped from wet leaves. In my study area in 1960, only territories 7, 8, 9, and 10 were not immediately adjacent to permanent water. The pairs of Bell Vireos in those territories presumably had to reply on wet vegetation for bathing.

VOCALIZATIONS

The male Bell Vireo begins to sing regularly soon after its arrival in spring. Some daily singing continues following the cessation of breeding activities until departure of the species in late summer or early fall. The highest sustained rate of song occurs on the first and second days of nest building. Because careful records of meteorological data were not kept, I cannot significantly correlate rates of song and specific temperatures and other weather conditions. Frequency of song was reduced when the temperature rose above 90° F., as it did on many days in June, 1960. Nice (1929:17) mentions a similar decrease in singing when the temperature exceeded 85° F.

Passerine birds typically sing at a high rate throughout courtship and nestbuilding, but at a markedly lower rate thereafter. Most vireos are atypical in this respect. In the study area in 1960 Bell Vireos sang more often than Robins, Mockingbirds, Field Sparrows, Brown Thrashers, Catbirds, and Doves breeding in the same habitat, about as often as the Meadow Larks in the adjacent fields, and less often than Painted Buntings.

The Bell Vireo seems to sing less often in the undisturbed state than when aware of the presence of an observer. Observations from my car, at a site approximately equidistant from territories 1 (1960), 2 (1960), 4 (1960), and 6 (1960) indicate that the rate of song during incubation is decidedly less when no disturbing influence is present. Normally, in this period, song aids in maintaining contact between the members of a pair, serving to locate the male as he forages. Mumford (1952:230) noted that the males often came out to meet him as he entered their territories, singing as they approached. The male typically continues to sing for some time after the intruder has departed. Here the song acquires the additional functions of alerting the female to danger and threatening the trespasser. Even after allowance is made for this reaction to disturbance, Bell Vireos sing more often than most of their nesting associates, and, on a seasonal basis, they are vocal for a much longer time.

Singing Postures

In the normal singing posture the body of the Bell Vireo is maintained at an angle of 35° to the horizontal. Occasionally, during nest building, I have observed the body held at angles as severe as 80° from the horizontal.

The head of the White-eyed Vireo is distinctly bobbed up and down, two or three times, during the utterance of a song phrase. A bob involves a deliberate withdrawal of the head towards the body and subsequent sharp, almost vertical, extension of the neck. The head of the Bell Vireo does not bob, although it vibrates as the song is delivered.

Flight Song

The Bell Vireo does not have a distinctive flight song; in fact, it rarely sings or calls while in flight. Nolan (1960:240) has recorded a male singing the normal song while in flight. Sharp scold-notes are uttered in mid-air when a bird is agitated or actually attacking an enemy. These notes and songs recorded by Nolan hardly qualify as flight song, for this term implies use of a distinctive vocalization not uttered in other circumstances.

Daily Frequency of Song

In the morning, Bell Vireos usually began singing a few minutes before sunrise. Their songs were invariably preceded in the study area by those of Western Kingbirds, Robins, Mourning Doves, Mockingbirds, Cardinals and Meadow Larks. Bell Vireos sang relatively little after 6:30 p. m., even on the longest days of the year. The latest daytime singing that was recorded was seven songs at 7:18 p. m. on June 20, 1960. A Cardinal in the vicinity sang for a full hour after this.

Types of Vocalizations

Six vocalizations were readily distinguishable in the field. These are divisible into songs and call notes.

1. Primary song. It has been described by Pitelka and Koestner (1942:103) as an "irregular series of harsh and sharp, but slurred notes preceded by a few distinct notes of the same quality and ending with a decided ascending or descending note of similar harshness." The terminal note may also be somewhat abbreviated and intermediate between an ascending or descending note. The song is sometimes delivered as a couplet that consists of a phrase ending on a descending note. This delivery is typical of incubation and later renesting. During early season activities, the bird utters

a phrase ending on the descending note as many as 15 times before a phrase ending on an ascending note is heard.

A sonagram of a single phrase, one of several recorded on May 9, 1960 (the third day of building of nest 1-b 1960), consists of 10 notes, the first of which is distinct. The remaining notes are slurred. This phrase is 1.4 seconds in length.

Songs are delivered most rapidly in the course of territorial disputes and defense. The song is loudest in times of nestbuilding and periods of aggressive behavior. At these times, on clear, calm days, the songs are audible 100 yards away. Singing in the nestling period and post-breeding season is audible at distances of no more than 50 feet; such notes have been termed "whisper songs." Table 1 summarizes singing rates at different periods of the nesting cycle in several situations and under various weather conditions.

Songs are of equal frequency in the immediate vicinity of the nest and elsewhere in the territory. Nice (1929:17) also found this to be true. Perches can be almost at ground level or as high as 60 feet. Forty per cent of my data on song concern singing at heights of more than 20 feet. As indicated in foraging, the lack of competition from aboreal species of vireos presumably contributes to the use of higher perches by Bell Vireos.

No female song was recorded in 1959, but on May 26, 1960, a female was heard to sing once. She appeared at nest 1-f (1960) shortly after the male arrived. Unlike him, she did not participate in building, but seemed to be inspecting the nest. After 30 seconds she sang once—a low garbled phrase—and also scolded once. After this she left. In the meantime the continuously singing male moved two feet away from the nest, then back to it and resumed construction.

The song of the female signaled to the male her departure. Pitelka and Koestner (1942:103) heard a female sing twice after she replaced the male on the nest. Females of three other species of vireos, the Black-capped Vireo, *V. atricapillus* (Lloyd, 1887:295), the Philadelphia Vireo, *V. philadelphicus* (Lewis, 1921:33), and the Latimer Vireo, *V. latimeri* (Spaulding *in* Pitelka and Koestner, 1942:103) have been heard singing. Lewis and Spaulding also suggest that the song of the female functions as a signal prior to exchange at the nest.

The primary song identifies the singer as a male Bell Vireo. It aids in securing a mate and in warning potential adversaries; also, the song is a signal in certain situations and serves to locate the male.

TABLE 1. REPRESENTATIVE SINGING RATES OF BREEDING BELL VIREOS. ALL RATES WERE AT AIR TEMPERATURES LESS THAN 86° F. EACH INSTANCE REPRESENTS APPROXIMATELY 30 MINUTES OF OBSERVATION.

Circumstance	Instances	Average rate per minute
Attraction of mate	2	6.3
Territorial dispute	5	12.8
Nestbuilding	6	7.0
Egglaying	1	3.0
Incubation	6	3.9
Exchange of partners in the incubation period	1	4.0*
Foraging	2	2.2
"Morning" song	1	28.6*
"Evening" song	1	1.9*
Over-all average rate per minute		6.3

* Not sustained; data representative of periods less than 5 minutes in length.

2. Courtship song. It is here termed the "congested" song and is comparable to the adult "run-on" song mentioned by Nolan (1960: 240). The congested song is a squeaky version of the primary song and is given when birds are engaged in pair-formation, nestbuilding, and egglaying. The delivery is rapid and the sound can be likened to that made by rapidly scraping a bow across a taut violin string. Nolan (*in* Mumford, 1952:230) is probably speaking of this song when he describes a "tuneless" song that "had a jerky, sputtering quality that characterizes part of the song of the Ruby-crowned Kinglet (*Regulus calendula*)." More recently (1960:240) he applies the adjectives "twanging," "Bobolink-like," "bubbling," "jerky," and "squeaky." This song is often blended with the primary song and is audible for 75 feet.

A specialized version of the congested song is associated with pre- and post-copulatory display but differs from the typical squeaky performance in terminating in two ascending notes reminiscent of the ascending phrase of the primary song.

3. Distress call. It was heard only once, when a captured bird was being freed from a net. When the bird was almost disentangled it uttered 10 high-pitched, plaintive notes. The quality of the notes suggested a relationship to the song phrase rather than to other types of vocalization. A nesting pair of Bell Vireos, 10 feet away, became extremely excited when they heard the distress notes. They "scolded" vigorously and flew around my head at a distance of six feet.

4. Alarm note. This is a specialized, three-note call of the male and was heard only from the onset of pair-formation through early nestbuilding. This whinnying, flickerlike call, phonetically *eh-eH-EH,* each succeeding note of which is louder than the one before, is given whenever the male is disturbed by an unfamiliar object. This call is generally succeeded by the *chee,* but occasionally blends into an extended "whinny," and is typically given from some perch affording an unobstructed view of the offending object. The male stretches his neck and cocks his head, the wings and tail are not flicked or fanned, and no feather tracts are erected. The bird, nevertheless, flits nervously from perch to perch when uttering the call.

5. The *zip.* The male has a special "scold" note of his own that is heard when an intruder first approaches the nest. Phonetically it is *zip-zip-zip.* It is not so loud as the *chee,* and the delivery is more deliberate than that note. If the intruder remains near the nest, the *zip* is usually replaced by the *chee.*

6. The generalized call note or *chee.* The call notes associated with several situations are combined under this subheading since all can be rendered in English by the same phonetic equivalent—*chee.* The *chee* associated with nestbuilding is of moderate pitch and delivered deliberately at a rate of about 40 per minute. The feeding call of the adults is a soft slurred *chee,* while that of the nestlings has a mewing quality. In general, the *chee* utilized in signal situations consists of a few repetitions of the basic note emitted at a moderate pitch. The *chee* associated with hostile and courtship behavior is higher pitched and the delivery is much more rapid, approximately 200 per minute. Nolan (1960:240) reports a continuous rate of 25 per five seconds when an adult Bell Vireo is alarmed. The *chee* of extreme anxiety is a loud emphatic buzz, phonetically ZZ-ZZ-ZZ-ZZ.

TERRITORIALTY

The Bell Vireo exhibits "classic" passerine territoriality. Within a specific area, a pair of this species carries out pair-formation, courtship activities, copulation, nesting, rearing the young, and foraging. With the cessation of reproductive activities, a pair continues to restrict its other daily activities to the same general area.

Establishment of Territory

In early May the segment of the total suitable habitat within which a Bell Vireo restricts its activities is not rigidly defined and the first male of the season ranges over an area too large to be maintained permanently—one that seems greatly to exceed the needs of breeding. Male 1 (1960), for instance, was first seen foraging over an area of approximately seven acres. With the influx of other males, portions of this large tract were usurped and the territory of the original male was gradually reduced to an area of little more than an acre.

In this initial period, a male becomes identified with a large area but is restricted to an area of nearly typical size by the encroachment of other males. Territorial disputes in this period often involve physical contact, as well as protracted sessions of high-intensity singing at rates exceeding three hundred song-phrases per hour.

Eventually the carrying capacity of the habitat is reached and no further partitioning occurs. The beginning of nestbuilding coincides with this relative stabilization of the territorial boundaries. Through the remainder of the cycle of behavior associated with any one nest, all activity is that of the occupant pair within its territory.

Size of Territories

The nine original territories established in 1960 varied in size from .26 acre to 3.1 acres (Table 2). Fitch (1958:270) found the territories of several pairs of Bell Vireos at the University of Kansas Natural History Reservation to vary from .4 to 1 acre. Hensley (1950:243) estimated the size of the territory of a pair of Bell Vireos observed in Piatt County, Illinois, at 3.1 acres. Nolan (1960:227) records home ranges of 2 to 3 acres. The pairs that he studied were sole occupants of fields several acres larger than the portions actually utilized. His description of the vegetation indicates that most of the second growth was not much taller than 7 feet. As indicated elsewhere, the second-growth in my tract averaged 15 feet tall. The smaller average size of territory (1.25 acres) that I found is probably a function both of this greater vertical range of available foraging area and the much higher gross density of birds (40 pairs per 100 acres).

Permanence of Territories

Most pairs remain in their original territories throughout the summer, although some shift certain territorial boundaries. In 1960 pairs 2 and 6, in the course of selecting a site for a replacement nest, annexed adjacent areas previously occupied by other pairs. Pair 2 relocated in a space that originally included territories 1 and 4, and pair 6 built a nest in an area formerly occupied by pair 7. Males 1 and 4 were sacrificed for specimens and pair 7 probably was destroyed by a predator. Owing to the presence of

TABLE 2. SIZE OF THE NINE ORIGINAL TERRITORIES OCCUPIED IN 1960.

Territory	Date first occupied	Dimensions
1	May 3, 1960	1.6 acres
2	May 5, 1960	.6 acre
3	May 7, 1960	.26 acre
4	May 11, 1960	1.03 acres
5	May 12, 1960	2.07 acres
6	May 14, 1960	3.1 acres
7	May 13, 1960	1.7 acres
8	May 14, 1960	.46 acre
9	May 14, 1960	.4 acre
		Average 1.25 acres

a nest, the annexed area becomes the focal point of the activities of a pair, but the original area is regularly visited and may be returned to in a later renesting.

Maintenance of Territory

Except in the early stages of nesting, territory is maintained primarily by song. In the period of incubation a male regularly patrols his territory between sessions of sitting on the eggs. He sings several songs from each of several perches. A male follows a predictable path, rarely traveling more than 150 feet from the nest. Incipient patrolling is seen early in the breeding season when territorial boundaries are in a state of flux.

The male White-eyed Vireo travels a semi-predictable route, as does the Solitary Vireo (R. F. Johnston, MS). According to Lawrence (1953:50), the male Red-eyed Vireo has a distinct singing area completely divorced from the nest area dominated by the female. Southern (1958:109), working with this same species in Michigan, did not recognize separate areas, but found that the male wandered randomly over the territory.

In a species so highly active as the Bell Vireo, the degrees of hostile action associated with an encounter overlap in such a fashion that no clearcut distinction can be drawn among the various displays. Nevertheless, certain generalized patterns are characteristic of all situations in which members of this species are in a state of anxiety. The threat displays described in the succeeding paragraphs may all be utilized within as little as two minutes; mutual agonism may be terminated at any stage by concerted attack of the dominant bird.

1. Vocal threat. When an intruder is discovered the resident male markedly increases his rate of singing. The alarm note, *eh-eH-EH*, is the first call uttered during the nestbuilding and egg-laying periods.

2. Head-forward threat. If the intruder does not flee, the resident male adopts a specific threat posture. The head and neck are extended. The feathers of the crown are erected, but those of the body are sleeked. The bird crouches slightly and the tail is flicked laterally, but not fanned. The intensity of the singing increases and is supplemented by scolding, also delivered at a rapid rate. The intruder normally retreats at this juncture.

3. Wing-flicking and submaximal tail-fanning. If the interloper remains, the anxiety of the resident male increases. He slightly depresses the tail and, at the same time, rapidly fans and closes it. The tail is only partially fanned. The wings are held slightly away from the body and rapidly flicked above the back. This flicking should not be confused with quivering of the wings associated with begging and other solicitory postures. Song is now almost completely replaced by high-intensity scolding. Associated with this high degree of anxiety are displacement behaviorisms, including bill-wiping, reversal of direction on a single perch, and a nervous hopping from one perch to another.

4. Ruffling and maximum tail-fanning. This display is most often seen in conjunction with the harassment of predators, but occasionally it is observed in territorial disputes occurring at the boundary of adjacent territories where neither male is strictly dominant and in which there is much vacillation prior to attack. The feathers of the abdomen are ruffled. The term "ruffled" pertains to a full erection of the feathers, giving a ragged appearance to the body outline (Morris, 1956:80). Ruffling of the abdominal feathers emphasizes their yellow color and seemingly heightens the intimidatory effect. The tail is fully fanned, and so maintained,

for a few seconds at a time; it is held at a 45° angle to the body. The scold becomes an extremely intense, stacatto buzz, ZZ-ZZ-ZZ-ZZ.

5. Supplanting attack. The attack directed against a trespassing male is initiated as a lunge that results in a collision with the opponent in mid-air or on his perch. The bird attacked is struck by his adversary's open beak or body.

Hinde (1952:71-72) indicates four courses of action followed by a Great Tit (*Parus major*) when attacked under similar circumstances. "(a) It flies away: The attacker usually flies after it and a chase ensues. (b) It shifts its perch a few inches: the attacker lands in its place, and both usually show head-up postures. (c) It remains where it is, but adopts a head-up posture: the attacker usually then shows upright flight. (d) It may fly up and meet the attacker in mid-air: in that case an actual combat may result, or both combatants may show upright flight."

Head-up posturing and upright flight are not presently recognized components of the behavior of the Bell Vireo. The behavior of the attacked Bell Vireo is similar to that described in (a), (b), and (d) above, and is clearly dictated by the proximity of his own "home base."

Eleven disputes among occupants of adjacent territories were witnessed between May 6 and June 3, 1960, in which some or all of the described threat displays were manifest (Table 3). In each instance, patrolling males were gradually attracted to each other. As they approached, their rates of song increased from an average of six repetitions per minute to 15 per minute. Eight of the disputes involved physical combat.

On May 6, 1960, when male 2 (1960) was in the process of usurping an eastern segment of the original territory of male 1 (1960), a violent, protracted dispute was observed. By this date male 1 (1960) had obtained a mate and had begun construction of nest 1-a (1960); male 2 (1960) had not yet acquired a mate. At first the two males were singing vigorously, from one to 10 feet apart. Female 1 (1960) followed her mate closely and scolded, at the same time partially fanning her tail. In the course of vocal dueling the males had traveled to within 50 feet of nest 1-a (1960), when male 1 (1960) suddenly lunged at 2 (1960). The males plunged to the ground, locking bills and clutching at each other with their feet as they fell. As soon as they touched the ground they separated.

Male 2 flew east with male 1 in pursuit. This conflict lasted three minutes.

Additional physical combat was witnessed several minutes later. This again involved striking with the bill, wings and feet. A high pitched squeaky *chee* was uttered by both combatants. The female scolded from a nearby perch. Upon separating, the males engaged in a wild, looping flight. At about 350 feet from nest 1-a (1960), the chase abruptly ended. For ten minutes thereafter, both males sang at a high rate from perches about 10 feet apart. This terminated the physical combat, but three additional protracted, vocal duels occurred in the remainder of the morning.

TABLE 3. INTRASPECIFIC DISPUTES IN MAINTENANCE OF TERRITORY.

	Number of conflicts	Behavior: Vocal dueling	Behavior: Combat	Average length of disputes
Prenesting	3	3	2	6 min. 40 sec.
Building	8	8	6	3 min. 8 sec.
Incubation	1*	1	.....	20 min.
Totals	12	12	8	5 min. 30 sec.

* Directed against a stuffed Bell Vireo.

Probably as a direct result of these conflicts, a neutral zone approximately 300 feet wide developed between the two territories. By May 14 this intervening area was occupied by male 4 (1960). By this date both 1 (1960) and 2 (1960) were involved in nest-building and 4 (1960) was not challenged for several days.

Maximum tail-fanning prior to attack also appears as an element of aggressive behavior in White-eyed Vireos. A brief skirmish between a male of this species and a small, greenish passerine was observed at the Natural History Reservation on May 25, 1960. The White-eyed Vireo was singing from a perch 30 feet high in a dead elm, when the unidentified passerine landed 10 feet distant. The white-eye ceased regular song and uttered several catbirdlike calls, and at the same time slightly depressed and fully fanned the tail. After 10 seconds, the white-eye lunged at the intruder, striking it in mid-air. A brief looping flight ensued through the branches of the elm before the intruder was able effectively to retreat.

Aggressive Behavior of the Female

The female Bell Vireo is concerned primarily with the defense of the nest and the young and she rarely assists the male in defense of distant parts of the territory. She employs the same threat displays as the male.

Interspecific Relationships

A number of meetings between Bell Vireos and other species were observed in the course of the study (Table 4). Resident pairs of this species exhibited different degrees of tolerance toward other

TABLE 4. INTERSPECIFIC CONFLICT OBSERVED IN 1959 AND 1960.

Species	Number of conflicts	Phase of breeding cycle	Behavior of Bell Vireos			
			HFT*	S	TF	A
Coccyzus americanus	1	Nestling period	.....	x		
Cyanocitta cristata	3†	Nestling and incubation period	x	x	x	x
Parus atricapillus	1	Prenesting	.....	x		
Molothrus ater	1	Nestling period	.....	x	.....	x
Dendroica petechia	1	Prenesting	.....	x	.....	x
Geothlypis trichas	1	Nestbuilding	.....	x	.....	x
Pituophis catenifer‡	1	Post-fledging	.....	x	.....	x

* HFT = head-forward threat; S = scolding; TF = tail-fanning; A = attack.

† Includes attack against a dummy Blue Jay.

‡ The Bull Snake is here included because the vireos directed typical aggressive displays towards it.

species. Many birds, including Cardinals, Field Sparrows, Painted Buntings and Mourning Doves were ignored completely. Chickadees evoked responses characterized by slight increase in song and some anxiety; this was perhaps owing to similarity in size, motion and call notes. Warblers, when met with, were invariably chased. They may be momentarily mistaken for rival vireos.

Blue Jays were vigorously attacked, especially late in incubation and throughout the nestling period of the Bell Vireo. I did not see a jay struck, but a vireo would circle one closely as it perched and pursue it when it flew, following as far as 100 yards beyond territorial bounds. The buzz, ZZ-ZZ-ZZ-ZZ, was uttered in conjunction with this harassment.

A stuffed jay placed eight feet from a nest elicited threat display and displacement behavior from the owners of the nest, but no

attack. Incubation had just begun at this nest. A dummy Bell Vireo placed close to another nest only momentarily disturbed the male, and the female completely ignored it. Incubation had also recently begun at this nest. At this same general stage, moreover, nesting pairs showed little inclination to harass me.

Discussion

Hinde (1956:341-342) indicates that territory has been defined in a number of ways by many workers. All of the definitions involve modification of Howard's classic "defended area." Pitelka (1959: 253) has reacted against this behaviorally-oriented concept. He thinks that the concept of territory should be based on exclusive use of an area by its occupants, and not so much the defense by which they maintain it.

Methods of treating territoriality in the Bell Vireo seemingly incorporate features of both schools of thought. The area used exclusively for all biological needs by a single pair of Bell Vireos is vigorously defended both physically and vocally early in the breeding season and vocally as the season progresses.

In the period of territorial establishment a relatively large area is actively defended. The building of a nest establishes a focal point of activity in a somewhat more restricted area than that originally occupied. After the success or failure of a nest, a new site is selected to which the focal point of activity is shifted. If suitable habitat adjacent to the extant territory is unoccupied by other Bell Vireos the unoccupied area may be annexed in the course of searching for a new site. Such annexation occurs only when pairs formerly occupying adjacent suitable habitat disappear from this territory; possibly the size of the territory of any one pair is dictated by the density of population of the species as well as by the presence of suitable habitat. This may not always be true as indicated by Kliujver (1951:40), who in studying the Great Tit, found no appreciable difference in the size of territory in two different habitats even though there was a marked difference in population density of the birds.

Fluctuation of territorial boundaries is not uncommon in passerines, especially when no rivals exist to contest movement. Hinde (1956:351) indicates that fluctuations in size of territory are to be expected although the territories of different species of birds have different mean sizes.

Once nesting activities commence there is a marked reduction in

the amount of territory utilized and a distinct decrease in the aggressive tendencies of the male; it would seem that energy previously utilized in regular fighting is rechanneled for nestbuilding, incubation and care of the young. Further, contraction of the area of activity obviates high-intensity territorial defense, as adjacent males, even in regions of high population density, are isolated from one another by an area no longer regularly traversed.

With cessation of breeding activities physiological mechanisms governing maintenance of territory seemingly are no longer active and yet the pairs of Bell Vireos remain within a restricted area which they alone use. Earlier definitions of territory as a "defended area" do not adequately cover such situations and yet from the standpoint of Pitelka the area still retains the characteristics of true territory. In fact, territory as defined by Pitelka is clearly manifest at this time. Whether the birds remain in an area through "force of habit" is of little consequence.

I have retained the term "territory" in preference to the term "home range" used by Nolan (1960:227). His failure to observe territorial defense is responsible for his terminology, although it is readily understandable that such defense would be lacking in a population of relatively low density in which pairs were isolated from one another by areas of unfavorable habitat. This isolation in itself would tend to preclude territorial conflict but territories were, in fact, maintained.

The marked similarity in the essential features of aggressive behavior in North American vireos attests to their close relationship. Flicking and fanning of the tail are distinct components of the hostile behavior of the Bell Vireo, White-eyed Vireo, Red-eyed Vireo (Lawrence, 1953:69), and the Black-whiskered Vireo (*Vireo altiloquus;* Bent, 1950:319), and, presumably, of the remaining species of the genus. The occurrence of these same displays as intrinsic behavioral elements of interspecific hostility suggests a common derivation. Moynihan (1955:256) indicates that all intraspecific hostile displays, and probably most interspecific hostile displays, evolved originally as social signals having the same general function. Further, Hinde (1956:344) points out that there is a fundamental similarity in the motor patterns used in fighting in different contexts, including both interspecific and intraspecific fighting.

COURTSHIP BEHAVIOR

The precise mechanism of pair-formation in the Bell Vireo is not known. My experience has been to find a male one day and then one or two days later to discover that it has a mate. Lawrence (1953:53), tells of a male Red-eyed Vireo singling out a female from a flock of migrants passing through his territory and violently driving her to the ground. Shortly after this attack the pair was seen searching for a nest site. But such an incident has not been reported for other vireos, nor have I witnessed such behavior myself.

Early courtship activities of the Bell Vireo are characteristically violent affairs, with the male directing strong aggressive attacks toward the female. Rapid, looping flights through the thickets occur, the female leading the male. Occasionally he deliberately collides with her in mid-air, but the pair quickly separate. This violent sexual chasing is manifest prior to the inception of nestbuilding. With commencement of this activity, sexual chases through the territory subside.

Absence of sexual dimorphism in the Bell Vireo obviously suggests that behavioral criteria are used by the birds in sex-recognition. The lack of aggression by the female upon initial aggression by the male is an essential component of recognition of sex; she is clearly subordinate. Such subordination is also the significant feature of continued sex-recognition. Courtship display by a resident male, directed toward a stuffed male and a wounded male which sat motionless, supports the contention that a subordinate or submissive attitude of the female is a key factor in sex-determination.

Nestbuilding and courtship are intimately associated in this species. The male constructs the suspension apparatus of the nest, the completion of which coincides with the assumption of nestbuilding activity by the female. Roles of the sexes in nestbuilding are described in the section on nestbuilding. The male frequently interrupts construction to court the female. This, in combination with perpetual song as he works, serves to strengthen the pair-bond and stimulate nestbuilding tendencies of the female.

It is doubtful that any attempts at copulation are successful up to this time. The female is singularly unresponsive to the advances of the male; a female retreats before most violent attacks and is seemingly oblivious to less vigorous behavior. After the female

assumes the responsibility of building, the tempo of courtship activities increases.

The female becomes increasingly more receptive and her work is often interrupted by advances of the male. Copulation occurs frequently from about the third day of nestbuilding through the first day of egglaying, a period of four to six days. Male displays and vocalizations associated with courtship continue through the fourth or fifth day of incubation.

Displays and Postures

The principal courtship displays and postures that were seen throughout the nestbuilding phase are as follows:

1. Greeting ceremonies. Both birds are crouched from one to five inches apart. The feathers on one (the male?) are sleeked, and on the other are fluffed. Fluffing (Morris, 1956:80) denotes partial erection of the body feathers producing a rounded, unbroken body line and is not to be confused with ruffling, mentioned in the sections pertaining to territoriality and pre- and post-copulatory display. Fluffing is generally considered to be an appeasement display and it is seen in a variety of situations involving a dominant-subordinate relationship. Both birds flick wings and tails rapidly and reverse directions on their perches frequently. A low, rapid *chee* is uttered during this performance. This ceremony is repeated often in the first three days of nestbuilding, but less frequently thereafter. It usually occurs after building by one or both partners and prior to another trip in search of nesting material. It lasts from 10 to 50 seconds and is not immediately followed by any additional courtship activities. Nolan (1960:228-229) observed mutual displays between periods of violent sexual chase that suggest that the greeting ceremonies that I have described are an integral part of pair-formation as well as a component of continued maintenance of the bond.

2. "Pouncing." The female rapidly quarter-fans and partially depresses her tail. She utters a high pitched scold (*chee*). The male, from a perch within two feet of the female, fans the tail fully and depresses it vertically, and, with mouth open, lunges at the female; or, with similar tail mannerisms, the abdominal feathers ruffled, the wings held horizontally, and the primaries spread, he sways from side to side from four to six times, and then lunges at the female. The male is silent when he pounces; the *chee* or the courtship song is emitted when swaying precedes pouncing. The male strikes the female with his breast or with his open beak. The female rarely flees although she is usually displaced several inches

along the branch upon which she is sitting. However, the female may fly several inches to a new perch. The failure of the female to adopt a solicitation posture presumably indicates sexual unreadiness. Instances of the male deliberately colliding with the female as she flies in the course of gathering nesting material are probably analogous to pouncing. In none of the above situations are females observed to fight back in any way. Nice (1943:174) believed pouncing to be analogous to sexual chasing found in such species as the Red-winged Blackbird. In the Song Sparrow, pouncing is observed most often in the first and second days of nestbuilding.

3. "Leap-flutter." The male, in the course of displaying with the tail fanned before the female, suddenly leaps eight inches to ten inches vertically and flutters in mid-air several seconds, before dropping to the original perch. This display occurs in full view of the female. It is often associated with pouncing and is also seen prior to copulation. In the latter instance it is probably pragmatically functional, for it permits the male to orient above the female before dropping to her back to copulate. No vocalization is uttered during the leap-flutter.

4. Pre-copulatory display (Fig. 3). The male faces the female. The tail is fanned fully and depressed at a sharp vertical angle to the body. Body feathers, both dorsal and ventral, are ruffled, almost tripling the apparent volume of the thorax. The head is withdrawn and slightly thrown back. Feathers of the head are not erected.

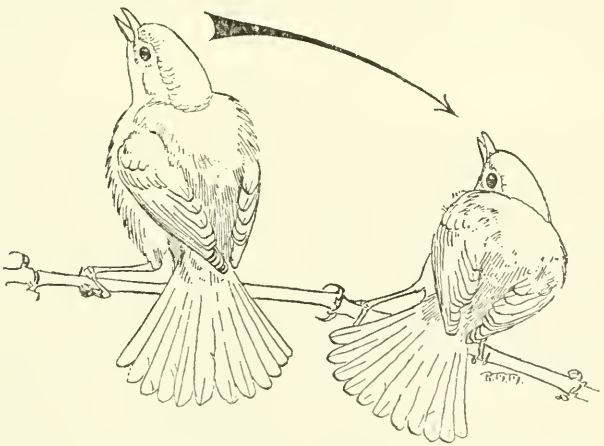

FIG. 3. A single male Bell Vireo in the pre-copulatory display. Note the ruffled dorsal and ventral body feathers. The male on the left has reached the zenith of a single swing. The male on the right has nearly reached the low point of a swing.

The mouth is opened wide. The legs are slightly flexed and the body is swayed laterally. Horizontally, the head and body traverse an arc of about 100°; vertically, they traverse an arc slightly less than 180°. At the low point of any one swing, the delivery of the courtship song begins. At the termination of the swing the two normal, ascending notes are emitted. This performance may last as long as three minutes.

The pre-copulatory display of the male elicits receptive behavior in the female. She crouches in a solicitous manner, with the body feathers fluffed and the tail raised slightly, and utters a muted *chee*.

5. Copulation. The male abruptly terminates his swaying display with a leap-flutter that positions him above the female's back. He then descends and copulation occurs. The male continues to flutter his wings to maintain balance throughout the two seconds of cloacal contact. Following an unsuccessful copulation on June 23, 1960, displacement preening and bill wiping were performed by both sexes.

6. Post-copulatory display. On June 25, 1960, after a second attempt at copulation with a stuffed bird in which semen was actually deposited on the dummy's back, male 10 (1960) performed a swaying display. In this instance, however, instead of addressing the dummy from the front, the male alighted one inch to the right of the stuffed bird. When swaying to the left (toward the dummy) the head of the displaying male actually passed above the neck of the stuffed bird. This ritualized behavior could conceivably be derived from hetero-preening.

Discussion

Within the scope of my research it was difficult to detect the over-all sequence of epigamic displays that result in synchronization of the physiological states of the sexes throughout the period of courtship. Possibly all displays, except the post-copulatory one, occur in no particular order in the courtship period. However, each ritualized display seemingly strengthens the pair-bond.

Swaying has been recorded in a variety of situations of a sexual and semi-sexual nature for the Solitary Vireo (*V. solitarius;* Townsend, 1920:158) and the Red-eyed Vireo (Tyler, 1912:230; Bent, 1950:342). In every instance the body feathers of the swaying birds were sleeked. Courtship behavior in any species of North American vireo seems closely to resemble that of any other; pairing

and nestbuilding of a female *V. solitarius* and a male *V. flavifrons* as reported by Hauser (1959:383) support the idea of close resemblance.

A marked similarity will be detected between certain basic elements of aggressive and epigamic displays. These basic elements are wing- and tail-flicking, tail-fanning, and high-intensity delivery of the *chee.* Pouncing and supplanting attacks are essentially similar. Such similarities suggest either a common origin for certain aggressive and epigamic displays or the derivation of one from the other.

High-intensity *cheeing* is obviously a function of excitement, whether in conjunction with hostility or sexual behavior. According to Andrew (1956:179), flicking of wing and tail in passerines are intention movements of flight. These actions have been emancipated from incomplete take-offs and incorporated in ritualized courtship and agonistic behavior. In incipient courtship behavior the male is governed by three conflicting tendencies; to flee, to attack, or to behave sexually before his mate (Tinbergen and Hinde, 1958: 256). When pairing, Bell Vireos interrupt sexual chase with "greeting ceremonies," the male's tendency to attack and the female's tendency to flee are momentarily reduced, and the forming bond is strengthened. Thus, the intention movements become an integral part of courtship.

In situations where attacking and fleeing are the two conflicting tendencies, wing-flicking and tail-flicking are incorporated into threat display, but do not lose all of their original function, for they facilitate attack. Tail-fanning, as a display element, increases the awesome aspect of the threatening bird and in courtship presumably makes the sexes more attractive to one another.

Courtship feeding has not been recorded for the Bell Vireo. In general, it is unknown in North American vireos, with the exception of the red-eye (Lawrence, 1953:53). It would serve no "practical" purpose in the Bell Vireo since the male regularly relieves the female during incubation, thus allowing her ample opportunity to forage. In the Red-eyed Vireo, only the female regularly incubates, and courtship feeding is definitely functional. Nolan (1960: 228) described a brief pecking or pulling with their bills between pairing birds. This may be incipient "symbolic" courtship feeding, or perhaps mutual preening.

SELECTION OF NEST-SITE AND NESTBUILDING

As far as can be determined, the nest-site is selected by the female. Typically, the pair makes short, low-level flights from tree to tree with the female invariably in the lead. The birds usually forage within each tree; the female interrupts this activity to inspect small forks of low, pendant branches and the male occasionally pauses to sing. The singing is loud but not particularly regular, as it is later when the male accompanies the female during actual nestbuilding. Method of selection of site resembles that described by Lawrence (1953:53) for the Red-eyed Vireo.

Nests are suspended from lateral or terminal forks about 27 inches high in bushes and small trees that, in the study area, averaged 11 feet, four inches in height (Table 5). The height above ground of the nests does not vary appreciably as the season progresses as is the case with nests of Red-eyed Vireos, for which Lawrence (1953:54) noted that late nests were placed higher than those built earlier in the season.

Most nests are so situated that they are protected and concealed by the dense foliage of trees. Where nests are placed in low bushes, as coralberry or dogwood, the bush is invariably overhung by the foliage of a much taller shrub or tree.

The nest tree or shrub was in every instance situated at the edge of a thicket or isolated from adjacent trees by several feet. Preference for open situations is characteristic of the species. In contrast, the nest of the White-eyed Vireo (Bent, 1950:229) is placed toward the center of thickets.

In the choice of sites in the study area, the Bell Vireos were almost unopposed by other avian species, owing to the size of the

TABLE 5. NEST-SITES UTILIZED IN 1960.

Plant	Number of nests	Average height of plant	Average height of nest
Ulmus americana	4	7 ft. 6 in.	2 ft. 3 in.
Maclura pomifera	20	13 ft. 11 in.	1 ft. 11 in.
Crataegus mollis	1	11 ft.	3 ft. 1 in.
Gleditsia triacanthos	2	15 ft. 6 in.	1 ft. 9 in.
Acer negundo	4	8 ft. 9 in.	2 ft. 5 in.
Cornus drummondi	2	8 ft.	2 ft. 8 in.
Symphoricarpos orbiculatus	3	3 ft.	1 ft. 10 in.
7	36	11 ft. 4 in.	2 ft. 3 in.

fork utilized and the fact that the nests are located peripherally, rather than centrally, in the bush or tree. This lack of competition for a nest-site provides a Bell Vireo with an ample supply of nest-sites within any one territory.

Selection of the first nest-site may take as long as two days, possibly owing to incomplete development of the nesting tendency, but more likely to a general lack of familiarity with the territory. Red-eyed Vireos require five to six days to choose the first nest-site (Lawrence, 1953:54). Later sites of the Bell Vireo are chosen in as little as three hours. Nest 1-c (1960) was abandoned at about 11:00 a. m. on May 14, 1960, when part of the thicket on the edge of which this nest was located was removed by brush-cutters clearing a power line right-of-way. By 2:00 p. m. this pair had begun construction of 1-d (1960) in an Osage orange 110 feet southwest of 1-c (1960).

This particular site is of further interest because it is the same one utilized for nest 1-a (1960). In all, four instances of utilization of a nest-site a second time were recorded. Two-a (1960) and 2-d (1960) were built in the same fork; 1-c (1960) and 1-h (1960) were in the same tree, but not the same fork. It should be mentioned that 1-a (1960) and 2-a (1960) were abortive attempts that did not progress beyond the suspension apparatus. Nice (1929:16) recorded a similar instance of the re-use of a nest tree, but different forks were used.

Re-use of an exact nest-site would ordinarily be impossible if the initial attempt were not abortive, because the presence of a completed nest would pose problems in construction with which the birds would probably be unable to cope. (A report by Morse *in* Bent, 1950:256 of a double nest indicates that this may not always be true. At the time of discovery one nest contained two eggs and the other nest contained young.) Since nests are used only once there would be no tendency to adopt the old nest. However, abortive nests, usually little more than a few strands of nesting material secured to the fork, might stimulate the birds to continue building. Re-use of a single nest-site in 15.8 per cent of 38 nests built in 1960 seems to be more than fortuitous circumstance. This re-use may have physiological benefits in conjunction with apportionment of energy for other nesting activities, because rapid location of a nest-site would mean that energy normally expended in searching and selecting could be rechanneled for actual construction. In each of the instances of rebuilding, the new nest was

begun on the same day that the previous nest was abandoned.

The re-nesting of pair 9 (1960) is worthy of note. These birds were established in the elm thicket on Clark land. Elm was by far the most abundant tree, with dogwood, Osage orange and honey locust also relatively common. There were only six boxelders in the territory and yet the four nests built by this pair were placed in them. This is the only instance of seeming preference.

Building

Nestbuilding by Bell Vireos can be best discussed in terms of the phases of construction described for the Red-eyed Vireo, Lawrence (1953:57), which are: (1) construction of the suspension apparatus, (2) construction of the bag, (3) lining of the bag and smoothing and polishing of the exterior, and (4) adornment of the exterior. Red-eyes (Lawrence, 1953:59) may continue adornment far into the period of incubation. Both the male and female Bell Vireo have been observed to add spider egg sacs and other silk to the exterior of the nest as late as the sixth day of incubation.

Nice (1929:16) recorded only the female Bell Vireo building, but she did recall, from previous studies, having seen males aiding somewhat. Pitelka and Koestner (1942:102) wrongly concluded that the female Bell Vireo builds unaided, but Hensley (1950:243) observed that both sexes participated in nestbuilding, and Mumford (1952:229) reported two instances of building by both adults. His description of the activities viewed in mid-May suggest that they were of the transitional period between the first and second phases. On the second occasion he recorded both adults building during the second phase. Since no details accompany this second observation I assume that it pertained to activity not necessarily typical of this phase of construction. Whereas both sexes of the Bell Vireo cooperate in building the nest, only the female Red-eyed Vireo builds according to Lawrence (1953:56). But Common (1934:242) saw both Red-eyed Vireos building a nest.

The suspension apparatus is constructed by only the male on the first day. He punctuates each trip to the nest with song. The single song phrase is given from three to eight times when the male, carrying nesting material in his bill, arrives in the tree. Typically, he alights on several perches within the nest tree before flying to the nest. He often interrupts his work with several songs; when he has finished adding a load of material he sings from several perches

within the nest tree before departing. The male periodically stops building to court the female.

In eight hours (494 minutes) of observing the first phase of construction at five different nests, I saw the female come to the nest 28 times; the male made 95 trips. The female came alone only once, and brought nesting material ten times, but did not build; on the other 18 occasions her visits were brief and she usually confined her activities to an inspection of the nest. Twenty of the visits by the female were made late in the first phase, marking a gradual transition to her assumption of building responsibility. (The delay by the female in beginning to build is puzzling; because all evidence indicates that she helps select the nest-site, I would expect her to help with the initial building. There seems to be no clear advantage in her delay in beginning to build.) The courtship and building activities of the male plus the presence of a partly completed nest seem to stimulate the female to commence building. Her visits become more frequent as construction of the suspension apparatus nears completion. At a time early in the second day the transition has taken place, and the female becomes the sole worker.

On May 7, 1960, male 2 (1960), at the time unmated, was observed as he came upon a nest of the previous year. The nest, after a year's weathering, suggested in appearance perhaps an early second-day nest. The bird flew to the nest and tugged and wove loose strands of grass for three minutes. Before leaving the site, the bird sang twice from different perches. This observation suggests that a partly constructed nest can elicit nestbuilding behavior, even in an unmated male.

The techniques of building by the male consist primarily of laying pieces of grass or bark across the fork, or along one of its branches, and then fastening them in place with pieces of animal silk. Once a "racket" has been formed, spider egg cases and plant down are emplaced among the fibers. The male employs weaving, twisting, and pecking motions of the head to emplace material.

As previously indicated, the female is the principal worker in the second and third phases of construction. The male infrequently visits the nest, but regularly visits the nest tree. The molding of the bag is accomplished by piling leaves, grasses and plant down onto the suspension apparatus. This material is also bound in with animal silk. As the amount of material accumulates, the female begins to trample it and gradually the bag takes shape. When trampling is

first attempted, the nest often fails to support the female and she falls through the bottom of the nest. Such an occurrence was observed on May 23, 1960, on three consecutive trips by female 1 (1960), in constructing nest 1-e (1960). As the bag deepens, additional strands of grass are added to the wall and woven into place.

The male is extremely attentive during this and the following phase. He follows the female as she gathers nest-material accompanying both this activity and her building with rapid song; he may give an average of seven song phrases per minute. The male brings to the nest a strand of grass, or some other material, about every twentieth trip. He frequently inspects the nest and the activities of the female from perches near the nest. Construction of the bag is ordinarily completed in the third day.

The third phase, the lining of the interior and the smoothing of the exterior, involves an additional one and one-half to two days. Smoothing of the exterior refers to tightening of the grasses woven into the bag and addition of more animal silk. In lining the nest, the female stands on one of the branches of the fork and emplaces one end of a long, thin strand of some relatively stiff piece of grass or strip of bark. She then jumps into the bag and, while slowly turning around, pecks it into place, thus coiling the strand neatly around the interior of the bag.

As previously mentioned, the fourth phase overlaps the periods of lining, smoothing, egglaying, and incubation. The principal activity is the addition of white spider egg sacs to the exterior. The trips are infrequent; but, occasionally, birds will interrupt an hour of incubation with three or four minutes of active adornment, during which several trips may be made. Both sexes participate in this phase.

Gathering of Nesting Material

Nesting materials were gathered anywhere within the territory. Occasionally materials were collected from within the nest tree, but usually they were obtained 20 to 200 feet from the nest-site. On several occasions I observed birds inspecting stems or branches where bark was frayed. Loose ends are grasped in the beak and torn free with an upward jerk of the head. Possibly the notch near the distal end of the upper mandible aids in grasping these strands. Plant down is first extracted and then rolled into a ball by means of the beak while held with the feet before being transported to the nest.

Length and Hours of Nestbuilding

As indicated by Nolan (1960:230), accurate determination of the length of nestbuilding is difficult because of continued adornment and polishing after the nest is functionally complete. Most of the early nests for which I have records took from four and one-half to five days to construct. A four- to five-day period of building is reported by other observers (Nice, 1929:16; Pitelka and Koestner, 1942:99; Hensley, 1950:242; Nolan, 1960:230).

One instance of protracted building was recorded. Nest 6-d (1960) was begun on May 29, 1960, and not completed until nine days later on June 6, 1960. In contrast nest 1-g (1960) begun on May 31, 1960, was finished three days later on June 2, 1960. Nestbuilding occurs between the hours of 6:00 a. m. and 5:30 p. m. Heavy rain in the early morning may delay building.

Abortive Nestbuilding Efforts

Eight of 38 nests started in 1960 were never completed (Table 6). Six of these abortive attempts were abandoned during, or shortly after, the completion of the suspension apparatus. Five of these nests were abandoned because the female did not begin building following the end of work by the male. The early abandonment of the other three nests 1-a (1960), 2-c (1960) and 6-e (1960) was attributable to the interruption of building by the male because of heavy rain and protracted territorial conflicts. The occurrence of these abortive nests at any time within the nesting efforts of a single pair indicates that such attempts are not examples of "false nestbuilding."

Renesting

Renesting after desertion or successful fledging occurs within two to thirty-six hours. Young were fledged from 1-a (1959) on June 19, 1959, and nest 1-b (1959) was discovered when late in the second phase of construction on June 22. If the nest was started on June 20, then renesting took place within 15 hours after fledging.

The Nest

Several authors have described various aspects of the nest of the Bell Vireo, notably Goss (1891:535); Simmons (*in* Bent, 1950:256), Nice (1929:13) and Nolan (1960:230-231). I can add but little to these descriptions.

The nest itself is a compact structure composed of strips of bark and strands of grasses that are interwoven and tightly bound with

TABLE 6. ABORTIVE NESTING ATTEMPTS IN MAY AND JUNE OF 1960.

Nest	Length of time worked on	Cause of abandonment
1-a	1 day	Heavy rain
1-h	2 days	Female failed to build
2-a	½ day	Female failed to build
2-c	1 day	Protracted territorial dispute
4-a	1 day	Female failed to build
5-a	1 day	Female failed to build
6-c	1 day	Heavy rain
7-a	2 days	Female failed to build

animal silk. The floor of the cup is first lined with a layer of small leaves and then the entire interior is lined with fine stems or strips of bark. Feathers are occasionally used to pad the bottom prior to lining, as are pieces of wool and milkweed down. Nest 2-e (1960) had been packed with small pieces of soil bearing moss prior to lining.

Early nests tend to be bulkier, having thicker walls and bottoms than later efforts. However, nests in May were found to have 16 per cent thicker bottoms and 41 per cent thicker walls than nests in June (Table 7). Standard nest measurements do not show this to be so, for the exterior and interior diameters at the rim are governed by the angle between the two branches of the fork.

TABLE 7. DIMENSIONS OF NESTS IN MAY (1960) AND JUNE (1960).

Measurements	May (N 10)	June (N 8)
External depth	61.6 mm.	59.3 mm.
Depth of cup	45.5 mm.	46.3 mm.
Outside diameter	57.3/55.5 mm.	54.3/53.5 mm.
Inside diameter	43.4/42.2 mm.	45.5/43.9 mm.
Thickness of forward wall 1 inch below rim	13.8 mm.	7.6 mm.
Thickness of bottom	11.3 mm.	4.6 mm.

EGGLAYING AND INCUBATION

Egglaying

Egglaying begins the first or second day after completion of the nest. The female sits in the nest occasionally for periods of five to twenty-five minutes on the day the nest is completed. This is interrupted by periods of nest-adornment and foraging; such activities sometimes keep the female off the nest for several hours. Prior to the laying of the first egg, only the female is seen on the

nest, although the male is often seen sitting quietly within the nest tree a few feet from the female. The infrequency of the "congested" song and the alarm (*eh-eH-EH*) after the inception of "broodiness" indicates the waning of courtship behavior. As later in incubation only the "normal" song and the scold are heard.

Eggs are laid early in the morning prior to 5:30 a. m. according to Nolan (1960:232). The nest is usually left unoccupied for considerable periods after the first egg is laid, but, on the first day of laying, both sexes have been observed sitting for brief periods averaging ten minutes in length. Eggs are laid at one-day intervals until completion of the clutch. I found incubation to begin with the second egg.

Clutch-size

The average clutch-size of the Bell Vireo in Kansas, based on thirty-three records, is 3.39 eggs (Table 8). Seasonally, the largest average clutches are produced in the middle of the breeding season, that is, in June. Lack (1947:308-309) indicates that in European

TABLE 8. AVERAGE NUMBERS OF EGGS PER NEST (NUMBER OF RECORDS IN PARENTHESES)*.

Year	May	June	July	Mean annual clutch-size
1959	3.0 (7)	3.2 (12)	3.0 (1)	3.06
1960	3.3 (6)	3.83 (5)	4.0 (2)	3.72
1959–1960	3.17	3.52	3.5	3.39

* These data have been supplemented from the literature pertinent to Kansas.

passerines the highest seasonal average clutch-sizes likewise occur in June. The largest average clutch-size in the Bell Vireo is presumably related to some aspect of the availability of food.

Caution is necessary in determining mean clutch-size in the Bell Vireo. Eggs occasionally disappear from the nest prior to or during incubation, without subsequent addition of cowbird eggs. Unfamiliarity with the history of such a nest on the part of the observer would lead to an inaccurate determination of clutch-size.

Complete clutches are not replaced with the same regularity as are nests. I have recorded intervals of six to thirty days between successive clutches. Successful replacement of clutches is determined by a number of factors: nest-site, completion of a nest, weather, predation, and parasitism by the cowbird. The difference

between the number of renesting attempts and the successful replacement of clutches seems to indicate that different physiological processes are responsible for these two phenomena and that there is lack of synchrony between them. The development of the ovarian follicle requires a specific number of days that is not always coincident with the building of replacement nests. If, in the Bell Vireo, replacing a nest were solely a responsibility of the female, instead of involving the male to a considerable extent, it would seem likely that replacement of nests and the replacement of clutches would be more closely coordinated.

Incubation

Nice (1954:173) considers the incubation period to be the elapsed time between the laying of the last egg in a clutch and the hatching of that egg, when all eggs hatch. My data indicate that, normally, intensive incubation begins when the second egg is laid and lasts fourteen days in the Bell Vireo. Nice (1929:99) also considered the incubation period in this species to be fourteen days but believed it to commence when the third egg was laid. Pitelka and Koestner (1942:99) noted that the first and second eggs hatched fourteen days after laying of the second egg. However, they thought incubation began with the first egg. This would mean a fifteen-day period for this egg. All the eggs that Nolan (1960:234) marked hatched in approximately fourteen days. Eight eggs artificially incubated by Graber (1955:103) required an average of 15.01 days to hatch. As Van Tyne and Berger (1959:293) indicate, periods of sitting on the nest, even all night, do not necessarily mean that incubation has begun, for it has been demonstrated in several species that birds may sit on an egg without actually applying heat. My own observations demonstrate that the first egg may be left unattended for several hours at a time on the day that it is laid.

The Roles of the Sexes in Incubation

Both the male and female sit on the eggs in the daytime. My study of histological sections of ventral epidermis indicates that the male does not possess a brood patch; the increased vascularization typical of the brood patch in females is not evident in males. But, the male loses most of the down feathers of the ventral apterium. Also, according to Bailey (1952:128), the male Warbling Vireo that sits on the eggs lacks a brood patch.

Bailey (1952:128) suggests that male passerines lacking brood patches that habitually sit on eggs do not heat the eggs. Thus it

cannot be considered true incubation since no increase of temperature in the eggs is effected by such means. He further notes that it is at night when eggs are likely to experience a drop in temperature that embryonic development will be impaired. I have no data directly pertaining to which sex sits at night, but it is presumably the female, because she is always seen on the nest early in the morning and late in the evening.

If a highly-vascularized brood patch is essential for true incubation, then it is surprising that males take regular turns on the nest in cold, rainy weather. On May 20, 1960, male 3 (1960) sat on the eggs longer than did the female (fig. 4). The temperature during

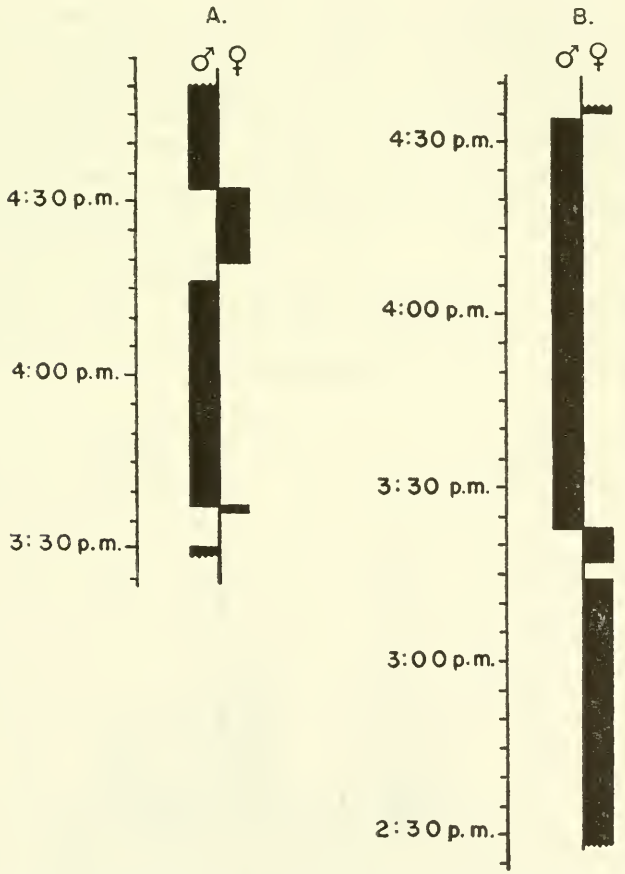

FIG. 4. Comparison of periods of incubation by both sexes in cold (54° F.) rainy weather (A) and in warm (82° F.) sunny weather (B).

this hour and a half of incubation was 54° F. One solution to this problem is supplied by Skutch (1957:74). He indicates that, "the type of the incubation is determined largely by innate factors, so that it persists through fairly wide fluctuations in weather, although it may break down in extreme conditions." Obviously then, in the example described above, the weather conditions do not qualify as "extreme." Sitting by the male is certainly functional to some extent for it relieves the female to forage; furthermore, the eggs are sheltered from inclement weather and protected from predators. Nolan (1960:232) suggests similar reasons for incubating by the male and adds the "conservation of heat supplied to the eggs by the female."

My data, based on incubation beginning with the second egg, indicate that the female incubates more often daily than the male (fig. 5). The male sits on the eggs only occasionally in the morning, but almost as often as the female in the afternoon. Nolan (1960:233) found that 95.5 per cent of the male's time on the nest and only 40 per cent of the female's time were attributable to the early hours of the day. Although I lack data on the critical hours of 5:00 a. m. to 6:59 a. m., I have enough observations (20) from 7:00 a. m. to 9:00 a. m. to indicate that the males sit on the eggs infrequently (3 of 20 instances) in those hours. The discrepancy in the two sets of data, which may be merely an artifact of sampling techniques, does suggest two possible alternatives: (1) the male

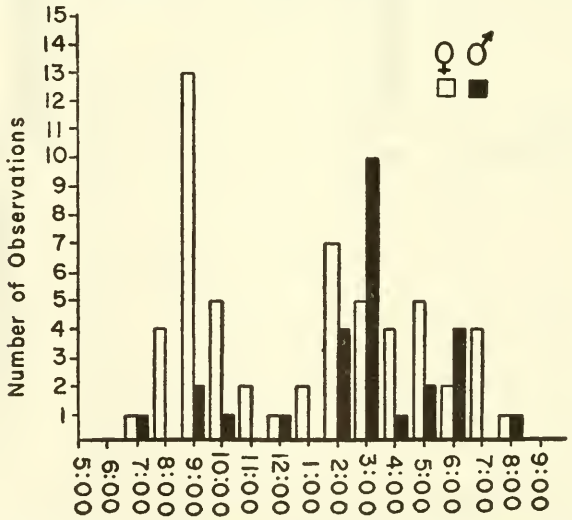

FIG. 5. Daily participation in incubation as indicated by the sex of the adult on the nest upon approach of the observer.

sits on the eggs in the morning and gives the female, who sits on the eggs throughout the night, an extended rest and an opportunity to forage; (2) the female continues to sit throughout the morning, especially during the early hours of daylight, a time of day when the temperature may still be low enough to impair development of the embryo.

Relief of Partners in Incubation

Relief of partners involves some ceremony. When the female is incubating, the male sings several times as he approaches the nest tree; the female responds with several *chees*, but otherwise remains immobile. The male sings several more times upon alighting in the nest tree whereupon the female *chees* again and flies directly from the nest. A few seconds later the male appears at the edge of the nest and, after inspecting the eggs, hops in and settles upon them. When the male is sitting he is notably anxious prior to an exchange with the female, often arising and craning his neck as he surveys the surrounding vegetation, seemingly searching for his mate. The singing of the male and the calling of the female serve as signals, coordinating the exchange.

NESTLING PERIOD

Hatching Sequence

As indicated earlier, hatching normally occurs fourteen days after the second egg is laid. Hatching of the young was staggered at three nests under observation. In nest 2-b (1959) the first young hatched on June 8, 1959, the second on June 10. In 3-b (1959) one young hatched each day from the 12th through the 14th of June. In 5-a (1959) two young hatched on June 15, the third on June 16, and the fourth on June 17. Size of the young differed notably for about three days as a result of staggered hatching, but after that day the younger birds tended to catch up in size with their older brood-mates. The fourth young in nest 5-a (1959) grew steadily weaker and was missing from the nest on June 23, 1959. Staggered hatching is usually thought to be related to the availability of food that will insure survival of at least some of the nestlings when a shortage of food exists. It is doubtful that staggered hatching has adaptive significance in the Bell Vireo, since there seems to be no shortage of food for the young. In small passerines such as the Bell Vireo the principal problem is to insure fledging as quickly as possible because of the danger from predators.

Development of the Nestlings

Young are pinkish at hatching and devoid of visible natal down. Du Bois (*in* Wetherbee, 1957:380), inspected day-old nestlings by means of a magnifying glass and was unable to detect any down. Nolan (1960:236) also indicates that the young are naked at birth and that the "body color is between flesh and rufous except where folds of the straw yellow skin obscure the underlying colors." The Hutton Vireo (*Vireo huttoni*) is essentially naked at birth, save for sparse hairlike down on the head and back (Wetherbee, 1953:380). The Red-eyed Vireo, according to Lawrence (1953: 67) is naked at birth save for a sparse covering of greyish natal down, on the head, shoulders, and back.

In the Bell Vireo the pterylae darken slightly on the second day and the color becomes more intense daily until the quills of the dorsal tracts, the wings, and the tail break from their sheaths on the sixth day. In Red-eyed Vireos the pterylae darken by the end of the first day and the quills break through the skin on the fifth day, erupting from the sheaths by the seventh day (Lawrence, 1953:67).

From the first day the young are able to squeak. Poking a young bird was sufficient to elicit this sound, phonetically a nasal *peek*. The only other vocalization noted throughout the nestling period was an abbreviated *chee*.

For the first three days tapping the nest or even movement of it caused by wind would elicit begging. By the fifth day at nest 2-a (1959) only vigorous agitation of the branch to which the nest was

TABLE 9. MATURATION OF NESTLING BELL VIREOS. THE FIRST DAY THAT AN ACTIVITY WAS OBSERVED IS SHOWN.

	Day of nestling life										
	1	2	3	4	5	6	7	8	9	10	11
Eyes open					x						
Feathers erupt						x					
Sound: Squeak	x										
Chee				x							
Begging	x										
Cowering								x			
Head scratching and Preening									x		
Hopping to rim of nest									x		
Fledging											x*

* This is the commonest fledging day.

attached evoked any response. At this nest on June 16, 1959, one young begged while the other cowered. Cowering is correlated with opening of the eyes, as the young bird that begged had its eyes only partly open. Both young cowered on June 19, 1959. Table 9 summarizes the maturation of the nestling Bell Vireos.

Parental Behavior

No eggshells were found in nests on the days of hatching. Presumably they had been removed by the parents. Nolan (1960:234) indicates immediate disposition of the eggshell after hatching. Lawrence (1953:62) suggests that conspicuous removal of eggshells by the female Red-eyed Vireo informs the male that the young have hatched.

Both sexes brood and the exchange of partners resembles that described for the incubation period. Decrease in brooding in the daytime begins about the sixth day of nestling life. Nolan (1960: 235) reports a sharp decrease in brooding when the oldest nestlings are seven days old. Brooding decreases notably on the sixth day of nestling life in the Red-eyed Vireo (Lawrence, 1953:62). Nice (1929:17), Hensley (1950:244), and Nolan (1960:235) report that the female Bell Vireo assumes a slightly greater role in brooding than the male.

Apparent sun-shading was noted at nest 3-b (1959) at 2:00 p. m. on June 17, 1959, on the fifth day of the nestling period. The nest contained three young. An adult flew to the nest; while standing on its rim the bird dipped its head into the nest six times, afterward appeared to be eating a fecal sac, than shifted position to the unattached portion of the rim, gaped three times, thereupon spread its wings, and sat motionless 35 minutes. In this attitude it formed an effective shield sheltering the young from direct sunlight penetrating the thin foliage of the honey locust in which the nest was situated. The temperature at this time was 95° F., but the sky was partly cloudy. By 2:30 p. m. the sky had become overcast and the sun passed behind a cloud. Although sunlight no longer fell directly upon the nest, the bird remained in the shielding posture for another five minutes before flying from its perch. Sun-shading was not observed at either of the other nests containing young; dense overhead vegetation protected those nests. Sun-shading has been noted in other species where the nest was poorly protected from the sun. Lawrence (1953:62) observed this behavior at two Red-eyed Vireo nests in conifers. The "sun-shield" posture of the Bell Vireo does not correspond to any of the sunning postures described by Hauser (1957).

Feeding of the Nestlings

Both sexes fed the young, and presumably began shortly after the first nestling hatched. My data indicate that the female does more feeding than the male (Table 10); in about eight hours of observation a total of 67 morsels were brought, 43 by the female and 24 by the male, for an average of once every 7.6 minutes. Nice (1929:17), however, observed a male to bring food 53 times as compared to 21 visits by the female. In five and one-half hours of watching, meals were brought once every 4.9 minutes. Du Bois (*in* Bent, 1950:257) recorded seven trips in an hour and forty minutes, or one every fourteen minutes.

At three nests containing young the adults were sometimes silent and sometimes vocal on their approach. The female often emitted a subdued *chee* which, coupled with the vibration of the nest caused by her arrival, elicited begging behavior from the young. None of the males was heard to utter such a call, but I have the impression that they often did call although I failed to hear the sounds. The

TABLE 10. FEEDING OF THE NESTLINGS.

Day of nestling period	Length of observation	Adult involved	
		Male	Female
1	30 min.	3	5
2	60 min.	1	4
3	60 min.	2	5
4	30 min.	1	4
7	60 min.	4	7
2	60 min.	3	3
6	60 min.	3	6
7	30 min.	3	3
9	60 min.	4	6
Totals	510 min.	24	43

males did, on occasion, sing several songs as they approached, even with food held in their beaks. Such singing elicited begging from the nestlings. Once the eyes of the young were open they often began begging when a silent adult was within two or three feet of the nest; begging behavior probably is elicited by tactile, auditory or visual stimuli in that order, or, as the nestling period proceeds, by any combination of these stimuli.

Not all trips made by parents resulted in successful feeding of young; some visits seemed to be purely for inspecting the young.

On other occasions the adults experienced difficulty in transferring food to the young, and, thus thwarted, would themselves eat the food. Nice (1929:17) estimated that from five to twelve of a total of seventy-five meals were eaten by adults.

Nest Sanitation

Both parents regularly removed fecal sacs from the nest, eating them for the first five days and thereafter carrying them off and presumably dropping them. It is doubtful that fecal sacs were actively removed in the last two days of nestling life as the bottoms of nests from which young flew away were invariably covered with excrement.

On several occasions a parent brought food to the nest and then remained perched on the rim alternately peering into the nest and then preening. Once bill swiping was observed and another time an adult male sang once. The adult remained at the nest from twenty seconds to a full minute.

Fledging

Eight young were fledged from the four nests in 1959. The nestling period lasted from nine to twelve days. Human interference may have been largely responsible for the fledging of the young at nine days. Pitelka and Koestner (1942:100) found nestling life to last eleven days. Nolan (1960:235) reports nestling periods varying from 10.5 to 12 days. The young Red-eyed Vireo is ready to leave the nest at ten days but often remains an additional day before departing (Lawrence, 1953:68).

The oldest nestling at nest 2-a (1959) hopped out on June 17, 1959, when I disturbed the parents. On this date the juvenal plumage was only partly developed and the young bird was incapable of flight. By the tenth day of nestling life the young in all the nests were observed to hop to the rim, flutter their wings, hop back into the nest and also to preen and scratch their heads. The young at fledging are usually completely feathered, but have notably short tails and relatively short, stubby wings. According to Ridgeway (1904:205) the juvenal plumage is much like that of the adult.

Nest Parasites

Pitelka and Koestner (1942:103) found that incubating adults and later the young suffered infestation of the northern fowl mite, *Ornithonyseus sylviarum*. Nolan (1960:241) reports a heavy infestation of this mite at four nests. Unidentified mites were noted at four nests in my study area in 1959. Incubating adults were ob-

served to peck at their breasts and scapulars from the eleventh through the fourteenth day of incubation. Serious infestations were not noted at the nests until the ninth day of nestling life. At this time the young were observed to scratch their heads and peck at their breasts, scapulars, and the base of their tails. On the day of fledging the nests were a seething mass of crawling mites; the mites also extended well up the branches to which the nests were attached. Nest 1-a (1959), which was discovered on June 18, 1959, presumably on the day after fledging, was densely covered with mites. Some mites were still crawling on this nest on June 20, 1959.

FLEDGLING LIFE

On June 20, 1959 I located one young 80 feet northeast of nest 2-a (1959), about five hours after it had left the nest. One parent was observed to feed it once. No young were seen thereafter from this or any other nest. Extreme agitation on the part of one or both parents on several occasions shortly thereafter, however, suggested the proximity of the young. Search in the immediate vicinity on each of these occasions proved fruitless. Three days after fledging their young, pair 2 (1959) was primarily occupied with courtship activities. Pair 1 (1959) was involved in courtship and nestbuilding one and one-half days after the apparent fledging of their young. Nolan (1960:238) indicates that the young remain within the territory and perhaps are fed by the parents up until an age of about 40 days. Sutton (1949:25) and Lawrence (1953:68) present contradictory reports on fledgling-parent relationships in the Red-eyed Vireo. Sutton concluded that the young quickly took leave of their parents whereas Lawrence reported a young bird being fed 35 days after fledging.

Second Broods

The curve based on 66 nesting records of the Bell Vireo representing the breeding activity in northeastern Kansas demonstrates a tendency toward double-broodedness (fig. 6). The peak of the breeding season is from May 20 to June 20. The large number (20) of replacement nests built in late May of 1960 tends to distort the curve of the breeding data; a second peak about 35 days after the first is evident.

I am of the opinion that the vast majority of vireos are single-brooded solely by virtue of the limited success of early nesting efforts, and that in "good" years most pairs would be double-

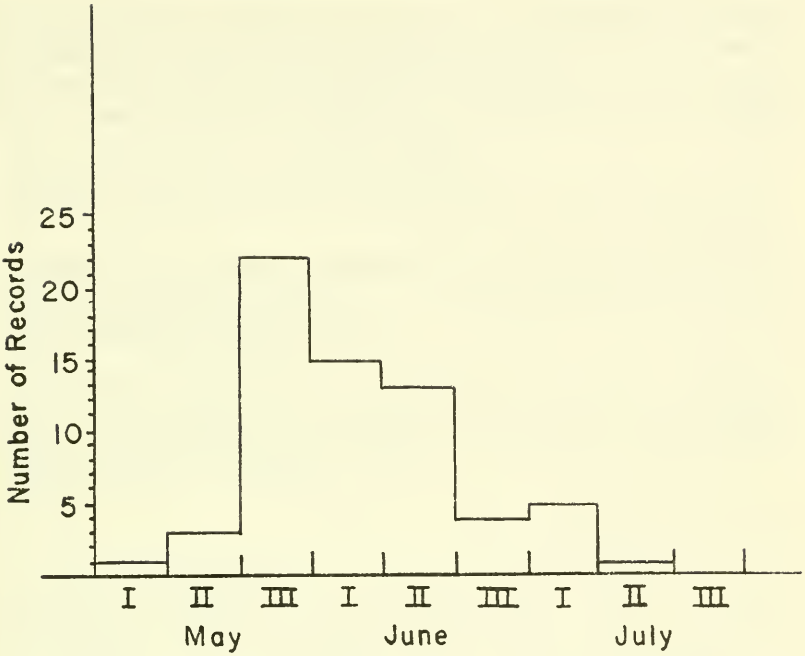

FIG. 6. Breeding season in northeastern Kansas based on the number of completed clutches in each 10-day period from May through July.

brooded. Each of the four pairs that successfully raised one brood in my study area in 1959 renested within a day or two after the fledging of the young. I do not know the fate of these nests. Nolan (1960:237) reports at least one instance of a second brood in the course of his study. Nolan (*op. cit.*) notes that the literature, in general, indicates that vireos are double-brooded, but that his evidence, mentioned previously, is the only evidence based on banded birds.

REPRODUCTIVE SUCCESS

Only four nests were successful; all of these were observed in 1959. The principal external factors responsible for nesting failure were severe weather, predation, parasitism by Brown-headed Cowbirds (*Molothrus ater*) and human interference (Table 11).

In late winter and early spring of 1960 heavy snow, continuously at a depth of at least 10 inches, covered most of the Mid-west from February 20 through March 20. Consequently, the growing season was some two weeks behind that of 1959. Of all the species in the

study area, the Bell Vireo is the most dependent on dense foliage for cover and concealment for its nests. Consequently the tardiness of the season seemingly negatively influenced reproductive success of this more than any other species of bird in the study area.

Behavior

Several aspects of the behavior of the Bell Vireo tend to contribute to nesting failure. They include:

1. Nest-site. Nests are occasionally suspended from exposed branches. Occurrences of this sort suggest that the dimensions of the fork are more important in the choice of a site than availability of cover.

2. Song. The loud, continuous song of the male during nest-building alerts cowbirds and predators to the presence of a nest. The incongruous habits of the male of singing in the nest tree and while sitting on the nest may facilitate location by some enemies, particularly cowbirds.

TABLE 11. EGG MORTALITY IN BELL VIREOS.

Mortality agents	N*	Eggs (N=29) 1959 Per cent	N	1960 Per cent
Predation	4	13.8	5	10
Weather	2	6.9	8	16
Cowbird	14	48.3	37	74
Totals	20	69†	50	100

* Number of eggs out of the total number laid lost to mortality agents.
† In 1959 nine eggs were successful (ultimately gave rise to fledglings).

I am not fully convinced that song from the nest is simply a "foolish" habit, since snakes, the principal predators with which this species has to contend, are deaf. My own field observations and the circumstances of the innumerable instances recorded in the literature of male vireos singing from the nest suggest that this is a function of the proximity of the observer. As mentioned elsewhere, vocal threat is the initial as well as the primary means by which territory is maintained. Song from the nest evoked by an enemy also serves to alert the female to danger.

3. Flushing. The Bell Vireo normally relies upon cryptic behavior to avoid detection at the nest. Most sitting birds, especially the females, either flush silently when an enemy is about forty feet

from the nest or remain sitting upon the nest tenaciously, refusing to flush even when touched or picked up. Some birds flushed at intermediate distances of from three to fifteen feet. In so doing they revealed the location of their nests. Since none of these "intermediate flushers" enjoyed nesting success there is possibly some correlation between these two factors.

Predation

Several complete clutches being incubated disappeared from nests that were unharmed. Absence of eggshells in the vicinity suggests predation by snakes.

On May 25, 1960, I found a *Peromyscus* climbing toward nest 1-a (1960). The mouse moved to within two inches of the nest whereupon I removed the mouse. Such small rodents constitute another potential source of predation.

Cowbird Parasitism

In this study the failure of 12 of 35 nests can be directly attributed to cowbird interference. It is well established that the incidence of cowbird parasitism of Bell Vireo nests is high (Friedmann, 1929:237; Bent, 1950:260-261). Nolan (1960:240) found only one nest of eight studied to be parasitized by cowbirds. He indicates that this is surprising in view of the heavy molestation of the Prairie Warbler (*Dendroica discolor*) in the same region. A possible explanation of this phenomenon seems to lie in the much greater abundance of the Prairie Warbler in comparison to that of the Bell Vireo. In my study area the incidence of cowbird parasitism on Bell Vireos in 1959 and 1960 greatly exceeded that of all other nesting species that were parasitized (Table 12).

As indicated previously, the female Bell Vireo leaves the nest unoccupied several hours at a time in the transition period between completion of the nest and the start of egglaying. Such behavior early in the morning certainly would facilitate deposition of cowbird eggs. Early in the nesting period the mere presence of a cowbird egg in the nest prior to the laying of the host's first egg leads to abandonment of the nest. This seems to be correlated with the relative strength of the nesting tendency; anyhow cowbird eggs laid in later nests prior to the appearance of the host's own eggs did not cause the nesting birds to desert. The Bell Vireo does abandon the nest when all but one of its own eggs have been removed by the cowbird. Mumford (1952:232) records the removal of a cowbird egg by the host birds and I recorded a similar instance

TABLE 12. INCIDENCE OF COWBIRD PARASITISM OF THE BELL VIREO COMPARED WITH OTHER PASSERINES IN THE STUDY AREA IN 1959 AND 1960.

	Bell Vireo	Other passerines
Total nests examined containing at least one host egg	35	43
Total nests parasitized	24	14
Total number of cowbird eggs	33	23
Per cent of nests parasitized	68.6	32.6
Total number of cowbird eggs per nest	.94	.54

involving nest 2-b (1960). On May 14, 1960, I found one punctured cowbird egg on the ground about 10 feet west of this nest. Occasionally a cowbird egg is buried beneath the lining of a nest. Mumford (1952:23) observed this in mid-May in 1951 and I observed pair 8 (1960) actively covering with building material a cowbird egg on July 5, 1960. Covering a cowbird egg constitutes effective removal. Since the egg cannot be turned, an adhesion develops.

The percentage of cowbird eggs hatched in relation to the number laid is relatively low. For instance, Mumford (1952:231) has only one record of a young cowbird successfully raised by a Bell Vireo. The data available in Bent (1950:260-261) also indicate that the percentage of cowbird eggs hatched is small. The Bell Vireo is less tolerant of cowbird parasitism than are many of the species so victimized, but is not so intolerant as the Robin, Catbird, and the Yellow-breasted Chat (Friedmann, 1929:193).

SUMMARY

1. The behavior of a small population of Bell Vireos was studied in the spring and summer of 1959 and again in 1960 in Douglas County, Kansas, and results are compared with previous studies elsewhere.

2. The Bell Vireo sings more often daily and throughout the nesting season than do the majority of its avian nesting associates. Six types of vocalizations are readily distinguishable in the field: primary song, courtship song, distress call, alarm note, specialized male call note or *zip,* and the generalized call note or *chee.*

3. Territories are established in early May and occupied throughout the breeding season and post-breeding season. The average

size of the territories in 1960 was 1.25 acres. Shifting of territorial boundaries occasionally occurs after nesting attempts.

4. Territory is maintained primarily by song, but at least five aggressive displays are manifest in the early phases of territorial establishment. These include: (a) vocal threat, (b) head-forward threat, (c) wing-flicking and sub-maximal tail-fanning, (d) ruffling and maximum tail-fanning, and (e) supplanting attack.

5. The precise mechanism of pair-formation in the Bell Vireo is not known. Early courtship activities are characteristically violent affairs. Absence of sexual dimorphism suggests that behavioral criteria are used by the birds in sex-recognition; the male is dominant and the female is subordinate.

6. The principal displays associated with courtship include: greeting ceremonies, "pouncing," "leap-flutter," pre- and post-copulatory displays, and the posture, copulation. The marked similarity between elements of courtship display and aggressive display suggests common origin or the derivation of one from the other.

7. The nest-site probably is selected by the female. Nests are suspended from lateral or terminal forks about 2 feet 3 inches high in small trees and shrubs averaging 11 feet 2 inches in height.

8. Nestbuilding is intimately associated with courtship and is a responsibility of both sexes. The male builds the suspension apparatus and the female constructs and lines the bag. Both sexes participate in adorning the exterior. Construction lasts from four and one-half to five days.

9. The nest is compact, pendant, and composed of strips of bark and strands of grasses that are interwoven and tightly bound with animal silk. Nests built in May are bulkier than those constructed later in the season.

10. Egglaying begins on the first or second day after the nest is completed. The eggs are deposited early in the morning. The average clutch-size of the Bell Vireo in Kansas is 3.39 eggs.

11. Both sexes sit on the eggs, but only the female truly incubates because the male lacks a brood patch. Incubation lasts fourteen days.

12. The Bell Vireo is double-brooded in "good" years.

13. Nesting failure resulted from severe weather, predation, parasitism by cowbirds, and human interference. Behavior that contributes to nesting failure is selection of an unfavorable nest-site, singing on and near the nest, and the tendency to flush from the nest in view of potential enemies.

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5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.
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10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.
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Two New Pelycosaurs from the Lower Permian of Oklahoma

BY

RICHARD C. FOX

University of Kansas
Lawrence
1962

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Two New Pelycosaurs from the Lower Permian of Oklahoma

BY

RICHARD C. FOX

In the course of examining material from fissure deposits of early Permian age collected from a limestone quarry near Fort Sill, Oklahoma, the author recovered several tooth-bearing fragments of small pelycosaurs. The fragments were examined, compared with descriptions of known kinds appearing in the literature, and determined to be new genera within the Nitosauridae (Edaphosauria) and Sphenacodontidae (Sphenacodontia).

Appreciation is expressed to Prof. Theodore H. Eaton, Jr., for permission to examine the collections of the University of Kansas from Fort Sill, and for the financial assistance furnished by his National Science Foundation grant (NSF-G8624). I am grateful both to Prof. Eaton and Mr. Dale L. Hoyt for their suggestions regarding this manuscript. The accompanying figures have been drawn by the author.

Family NITOSAURIDAE

Delorhynchus priscus new genus and new species

(*delos*, Gr., evident; *rhynchos*, Gr., neuter, nostril; *priscus*, L., ancient. *Delorhynchus* is masculine because of the ending that it acquires when transliterated into Latin.)

Type specimen.—Fragmentary left maxilla, bearing four teeth, KU 11117.

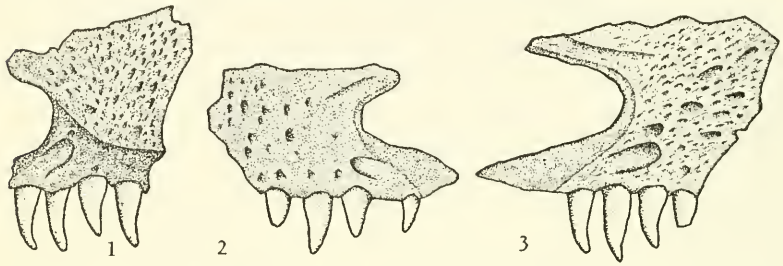
Referred specimens.—Fragmentary right maxilla having four teeth, KU 11118; fragmentary left maxilla having four teeth, the most posterior of which has been broken, KU 11119.

Horizon and locality.—A fissure deposit in the Arbuckle limestone at the Dolese Brothers Limestone Quarry, approximately six miles north of Fort Sill, in sec. 31, T. 4 N, R. 11 W, Comanche County, Oklahoma. These sediments are of early Permian age, possibly equivalent to the Arroyo formation, Lower Clear Fork Group of Texas (Vaughn, 1958: 981).

Diagnosis.—Small; marginal teeth conical, slender and recurved at tips; marginal tooth-row without caniniform enlargement; narial opening enlarged and bordered dorsally, posteriorly and ventrally by maxilla; maxilla with foramen opening laterally at posteroventral corner of naris.

Description (based on 3 maxillary fragments, see Table 1).—Each of the maxillary fragments bears four thecodont teeth. These are conical, slender and sharply pointed; in their distal third they are slightly recurved, laterally compressed, and have anterior and posterior non-serrated cutting edges. In medial aspect at their bases, the teeth are longitudinally striated. The bases of the teeth

are circular in cross-section and are slightly bulbous. There is no caniniform enlargement of any of the teeth, the longest tooth of each fragment being differently placed in the series of teeth and little longer than the others. There is no swelling on either the internal or external surfaces of the maxillae. The teeth are in a continuous series; no diastema or maxillary step is evident.



FIGURES 1-3. *Delorhynchus priscus*, lower Permian, 6 miles north of Fort Sill, Comanche County, Oklahoma. All × 3.

FIG. 1. KU 11117 (type specimen), lateral view of left maxilla.
FIG. 2. KU 11118, lateral view of right maxilla.
FIG. 3. KU 11119, lateral view of left maxilla.

The fragments have been broken along similar lines of fracture, and each is approximately rhomboidal in shape. The maxilla encircles the posterior border of the naris and extends dorsally above the naris to an extent sufficient to indicate the probable exclusion of the lacrimal bone from the narial border. At the posteroventral corner of the naris a foramen opens onto the lateral surface of the maxilla. The opening is the entrance to a canal that runs posteriorly

TABLE 1.—DIMENSIONS, IN MILLIMETERS, OF THREE MAXILLARY FRAGMENTS OF DELORHYNCHUS PRISCUS

CATALOGUE NUMBER AND MEAN	Anterior height of fragment	Posterior height of fragment	Length of fragment at tooth-row	Dorsal length of fragment	Mean length of teeth	Anterior width of naris
KU 11117	6.0	8.0	6.0	8.0	3.0	3.0
KU 11118	6.0	6.0	9.0	8.0	2.0	3.0
KU 11119	6.6	8.0	10.0	11.0	?	4.6
Mean	6.2	7.3	8.3	9.0	2.5	4.5

above the tooth-row throughout the length of each specimen. Beneath the naris the maxilla extends as a broad tapering shelf, the ventral surface of which articulates with the premaxilla. The narial rim is wide, but wider ventrally than dorsally. The plane of the narial rim is oblique to the lateral surface of the maxilla. The external surface of each fragment is grooved and pitted. The ossification of each fragment appears to have been complete.

Discussion.—The Nitosauridae are small primitive edaphosaurs with a moderately elongate face, sharp subisodont teeth, little development of canines and few specializations. The jaw is of a primitive type and articulates on a level with the tooth-row. The palatal dentition is primitive (Romer, 1956:280). The nitosaurids are thought to be related to the later Caseidae, and the most obvious structural similarities are found in the postcranial skeleton (Vaughn, 1958:989). Cranial resemblances between the families are fewer, but nevertheless indicate that a nitosaurid-caseid relationship exists.

Vaughn (1958) described a small pelycosaur, *Colobomycter pholeter* (Eothyrididae, Ophiacodontia) that structurally resembles the Caseidae. This individual also was obtained from the Fort Sill locality. In Vaughn's opinion the features of *Colobomycter* indicate a close relationship between eothyridids and caseids and the possibility that the caseids may well have been of eothyridid rather than nitosaurid derivation.

In view of this historical uncertainty of the relationships between the Nitosauridae, the Eothyrididae and the Caseidae, it is well to consider how the maxillary fragments described above differ from and resemble representatives of each of these three families as reported in the literature.

Delorhynchus resembles *Colobomycter* in size. The mean extramaxillary length of the undamaged teeth of the three fragments is 2.5 mm., equal to that reported by Vaughn (1958:985) for teeth about midway in the postcanine series of *Colobomycter.* None of the teeth of *Delorhynchus* extends beyond the maxillary rim as far as does the canine of *Colobomycter* (3.5 mm.).

The teeth in both genera are conical and sharply pointed. The naris in each is enlarged, and the lacrimal is excluded from the narial margin in each (by inference in *Delorhynchus.*)

The differences between the maxillae of *Colobomycter* and *Delorhynchus* are most striking in the lack of canines in the latter and the correlated absence of modifications of the maxillary for support of canines. Additionally, *Delorhynchus* bears an infraorbital canal

in contrast to the groove in similar position in *Colobomycter*. The recurvature of the four teeth present in the fragments of *Delorhynchus* differs from that in the teeth of *Colobomycter* in which only the canine and precanine are recurved. Vaughn implies that anterior and posterior cutting edges extend the length of the teeth in *Colobomycter*; these are restricted to the distal third of the teeth in *Delorhynchus*. The external surfaces of the maxillae of *Delorhynchus* are pitted and ridged; Vaughn was unable to discern sculpturing of the corresponding surfaces in *Colobomycter*.

Delorhynchus resembles the nitosaurids in size, the shape and sharpness of the teeth, their recurvature and the slight enlargement of their bases, the exclusion of the lacrimal bone from the narial margin (in *Mycterosaurus*) and the apparent lack of a special canine pair of teeth. Resemblances to the caseids are to be noted in the enlargement of the naris (4.5 mm. in height as opposed to 1.7 mm. in *Colobomycter*), lack of development of canines, presence of an infraorbital canal (in *Cotylorhynchus*) and absence of many replacement gaps in the marginal row of teeth.

The absence of caniniform enlargement and the extension of the maxilla dorsad of the naris exclude *Delorhynchus* from the Eothyrididae (Ophiacodontia) but are no bar to its inclusion in the Nitosauridae (Edaphosauria). The marginal teeth of *Delorhynchus* are simple and primitive, being much like those of the nitosaurids that are described in the literature.

The large narial opening and its posterior, dorsal and ventral enclosure by the maxilla, the infraorbital canal, and the sculptured external surfaces of the maxillary fragments indicate that *Delorhynchus*, in these features at least, is close to achieving the caseid grade.

Family SPHENACODONTIDAE

Thrausmosaurus serratidens new genus and new species

(*Thrausmosaurus* is formed from the neuter Greek noun, *thrausma*, meaning fragment, and the masculine Greek noun, *sauros*, meaning reptile. The specific name, *serratidens*, is formed from the Latin *serratus*, meaning serrate, and the masculine Latin noun, *dens*, meaning tooth. The specific name is used as a substantive in apposition with the generic name.)

Type specimen.—Fragmentary left dentary, bearing five teeth, the most posterior of which is broken at the base, KU 11120.

Referred specimens.—Fragmentary ?left maxilla, having two teeth, KU 11121; fragmentary left dentary having two teeth, KU 11122.

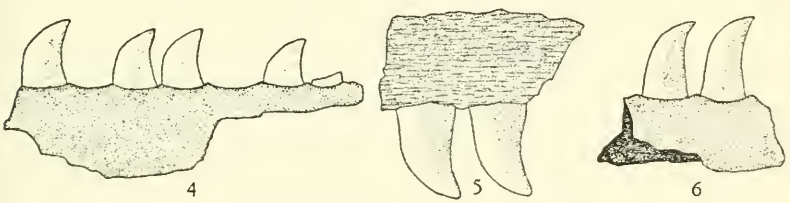
Horizon and locality.—From the early Permian fissure deposits in the Arbuckle limestone of the Dolese Brothers Limestone Quarry, approximately 6 miles north of Fort Sill, in sec. 31, T. 4N, R. 11 W, Comanche County, Oklahoma.

Diagnosis.—Small; teeth thecodont, compressed laterally, recurved distally, and bearing anterior and posterior cutting edges; anterior serrations limited to recurved portions of teeth, posterior serrations extending nearly entire length of teeth; lateral compression of teeth more pronounced medially than laterally; bases of teeth expanded.

Description.—The type specimen is 16 mm. long. It bears five teeth that are implanted in a straight row. Empty sockets are present between the first and second teeth, and the third and fourth teeth. The first tooth is 3.0 mm. long, the middle two are each 2.5 mm. long, and the fourth tooth is 2.0 mm. long. The fifth tooth is broken off at its base.

The empty sockets are large. The mouth of each is circular and approximately 2.0 mm. in diameter. Both sockets are 1.25 mm. deep. The bases of the teeth are expanded to fill the sockets, although the blades of the teeth arise from only the lateral portions of the bases. The edge of the dentary rises above the bases of the teeth medially, thereby producing a small depression at the junction of each base with the dentary bone.

The lateral compression of the teeth is pronounced but asymmetrical, in that the lateral surface of each blade is more convex than the medial surface.



FIGURES 4-6. *Thrausmosaurus serratidens,* lower Permian, 6 miles north of Fort Sill, Comanche County, Oklahoma. All × 3.

FIG. 4. KU 11120 (type specimen), lateral view of left dentary.
FIG. 5. KU 11121, lateral view of ?left maxilla.
FIG. 6. KU 11122, lateral view of left dentary.

The recurvature of the anterior cutting edges is much more severe than that of the posterior edges, but the recurvature of both is limited to the distal half of each tooth.

The serrations of the cutting edges are not visible to the naked eye and are limited on the anterior edges of the teeth to those portions of the blades that are recurved. The posterior serrations extend nearly to the junction of the blade of each tooth with its base. The serrations tend to be more nearly crenulate than cuspidate.

A portion of the lateral wall of the dentary surrounding the Meckelian canal is present. The external surface of the wall is gently convex and smooth, without sculpturing. The internal surfaces of the canal are unmarked either by muscle scars or foramina.

The fragment is a piece from the posterior portion of the dentary, since the decrease in height from the first tooth to the fourth is pronounced.

KU 11122, a fragment of the left dentary bearing two teeth, is 7.5 mm. long. The anterior tooth is 3.0 mm. long; the posterior tooth is 3.5 mm. long. The shape of the teeth and their implantation conform to the description of the type specimen. The lateral surface of the fragment is smooth and gently convex. What little is present of the surface bordering the Meckelian canal is unmarked.

The ?maxillary fragment bears two teeth which are 3.0 mm. long, and which conform in their characters to the type. The lateral, medial and ventral surfaces of the fragment have been sheared off, so that an exact identification of the bone is impossible. Presumably the fragment is too deep dorsoventrally to be a piece of the dentary, and no sign of the Meckelian canal is present.

Discussion.—The implantation, lateral compression, recurvature and cutting edges of the teeth borne by these fragments make clear their sphenacodontid nature. The characters of the fragments are too few to determine subfamilial affinities, however. That the fragments are the remains of adult animals can be only surmised from the lack of bones or teeth of large pelycosaurs in the extensive collections of the University of Kansas from the Fort Sill locality.

If *Thrausmosaurus* is, in fact, adult, the genus is an unusually small sphenacodontid, and of significance both on that account and because of the resemblance of the teeth presently known to those of its far larger relatives.

The Fort Sill Locality.—Peabody (1961) suggested that the fissures of Fort Sill had been used as dens by predatory animals in the early Permian, and that the unusually abundant bones in the fissures were the remains of animals eaten there by these occupants. Evidence now known to me affords an alternative explanation that is presented here as a preliminary to a more complete study of the fauna and paleoecology of these deposits currently being undertaken.

The suggestion that the skeletal material found in the fissures is the remnant of the prey of other animals is questionable because of:

1. The absence of tooth marks on the fossils.
2. The recovery from the matrix of skulls and portions of articulated skeletons that are undamaged or damaged only by pressure after burial.
3. The rarity in the deposits of animals of larger body size than *Captorhinus,* the exceptions being a few limb fragments and skull fragments of labyrinthodont or pelycosaurian nature.
4. The absence of coprolites in the matrix.

If the fissures were the dens of predators, at least some and probably many of the bones would show tooth marks. A predator feeding on other animals would be expected to leave some evidence of its habits on the bones of its prey. No such evidence is known to me, either from my own examination of several thousand bones or from the reports in the literature by others who have studied aspects of the early Permian fauna of Fort Sill.

If the predators were larger than *Captorhinus* and occupied the fissures for a long enough time to account for the accumulation of the tremendous numbers of individuals that are represented, a considerable amount of the skeletal material of the larger animals would be present in the fissure deposits. Even if for some reason the predators died in areas other than within the fissures, thereby accounting for the absence of large bones, coprolites should appear in the deposits if, in fact, the fissures were feeding places. In view of the nearly undamaged condition of many of the bones recovered from the fissures, it is reasonable to expect that fecal material would be preserved.

The character of the matrix of the deposits varies from a homogeneous clay to clay interrupted by layers of soft, limey, conglomeratic rock, to a hard, well-cemented, calcareous conglomerate. In general the bone in each kind of matrix is colored characteristically and exhibits a characteristic degree of wear. The bones entrapped in the homogeneous clay are relatively few, black, usually disarticulated, little worn and not unduly fragmented; consequently the discovery of undamaged limb bones, for example, from this kind of matrix is not unusual. The bones found in the stratified portion of the matrix are more numerous within the layers of conglomerate than between. The bones are black, brown or white, highly fragmented and waterworn to a variable degree. The fragments recovered from the hard, calcareous matrix are numerous, range in color from white through various shades of brown, to black, are highly fragmented, and are usually worn by water.

These categories for bone and matrix, however, are not mutually

exclusive, since bones of any of these colors and exhibiting any degree of wear and fragmentation are found in any of the kinds of matrix described above. That water was the agent of wear is suggested by the highly polished appearance of the worn bones and pebbles that are found in the matrix.

The variability of the matrix and of the color and condition of the bones indicates that the agencies of burial and fossilization differed from time to time and that the agency of transportation of the bones from the site of burial to the fissures was running water. One can easily visualize a stream coursing the early Permian landscape that was subject to periodic flooding and droughts. Along the banks of the stream and in its pools lived a variety of microsaurs, captorhinids, small labyrinthodonts and small pelycosaurs. Some of the animals, after they died, were either buried near the site of their death or were swept along and buried in sediments further downstream. Burial was for a length of time sufficient to impart a color to the bones characteristic of the site in which they were buried. Later floods reexposed the sites of burial, picked up the bones and carried them to the openings into the fissures. Presumably, too, a proportion of the bones was carried to the fissures without previous burial.

The differences in wear exhibited by different bones within the same block of matrix is attributable to differences in distance that the bones were transported before final deposition. The final sites of deposition, the fissures, were inundated occasionally by floods alone, or because of changes in location of the channel of the stream at the time of flooding. The periodicity of deposition of the sediments within portions of the fissures is indicated by the stratification of the bone conglomerate mentioned earlier.

In summary, it seems that there is little or no evidence beyond the numbers of bones involved to support the hypothesis that the concentration of bones in the fissures of Fort Sill represents the remains of food of predators, and that the fissures were used as dens by their predatory occupants. On the contrary, the evidence indicates that the deposition of the bones in the fissures was secondary and that the agency of transportation, deposition and accumulation of the bones was an early Permian stream characterized by periodic flooding.

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Vertebrates from the Barrier Islands of Tamaulipas México

BY

ROBERT K. SELANDER, RICHARD F. JOHNSTON,
B. J. WILKS, AND GERALD G. RAUN

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Vertebrates from the Barrier Island of Tamaulipas, México

BY

ROBERT K. SELANDER, RICHARD F. JOHNSTON, B. J. WILKS, and GERALD G. RAUN

Lying between the Gulf of Mexico and the Laguna Madre de Tamaulipas is a narrow barrier island extending from the delta of the Rio Grande south for 140 miles to within 185 miles of Tampico, Tamaulipas (Plate 5). This island, like most of coastal Tamaulipas, has been all but neglected by zoological collectors. Consequently, little is known of the kinds, distribution, and seasonal status of the vertebrates occurring there. The present paper is a report on land vertebrates collected and observed on the northern part of the barrier island of Tamaulipas from July 6 to 10, 1961. Our collection, which has been deposited in the Museum of Natural History, The University of Kansas, consists of 63 reptiles, 33 mammals, and 97 birds (58 skins, 19 skeletons, and 20 alcoholics).

Acknowledgments

We are especially indebted to Dr. Charles H. Simpson of Sinton, Texas, who generously placed at our disposal his truck, a four-wheel drive "Land Rover," without which travel on the island would have been difficult. We also acknowledge a loan of field equipment provided by Dr. Clarence Cottam, Director of the Welder Wildlife Research Foundation, Sinton, Texas.

Financial support for the present research was provided by grants from the National Science Foundation to The University of Texas (G 15882) and to The University of Kansas (G 10043).

Permits to collect vertebrates in México were supplied by Ing. Luis Macias Arellano, El Director General, Departamento de Conservación de la Fauna Silves, México, D. F.

We are indebted to Dr. Richard H. Manville for arranging a loan of specimens of *Geomys personatus tropicalis* in the United States National Museum. Dr. Marshall Johnston kindly identified specimens of plants from the barrier island. Several bones of birds and mammals were identified by Dr. Pierce Brodkorb and Dr. E. L. Lundelius. Mr. J. Knox Jones identified some of the mammalian material, and Dr. W. E. Duellman verified the identifications of the lizards; we thank all of these men for their willing assistance.

The Ecological Setting

The barrier island of Tamaulipas geologically and ecologically resembles Padre Island, of the Gulf coast of lower Texas, north of the mouth and delta of the Rio Grande. South of the delta, the island in Tamaulipas is a narrow strip of sand less than a mile in average width and is broken by a series of narrow inlets or "passes" through which water from the Gulf of Mexico mingles with that of the Laguna Madre de Tamaulipas. The passes are subject to recurrent opening and closing. North of the mouth of the Río Soto la Marina, eight passes are designated by local fishermen, but only three, the Third, Fourth, and Fifth, were open at the time of our visit.

The Laguna Madre de Tamaulipas is described by Hildebrand (1958) in connection with a preliminary study of the fishes and invertebrates there. The average depth is probably less than 70 cm. and the waters are hypersaline. In the time of the recent drought in Texas and northeastern México, salinity varied from 108 to 117 parts per thousand in the northern part of the laguna near Arroyo del Tigre (measurements taken in March, 1955) to from 39 to 48 parts per thousand in the southern part near Punta Piedras (measurements taken in October and November, 1953, and in March, 1954). Discussions of the geologic history, ecology, and zoogeography of the lagoons of the Gulf coast of the United States are given by Hedgpeth (1947; 1953).

Localities in coastal Tamaulipas mentioned in the text of this paper are shown on Plate 5.

The principal animal habitats are found in three vegetational associations (plates 6 and 7). On flats and low dunes lying between, and partly sheltered by, larger active dunes, small clumps of *Croton punctatus* and a sedge (*Fimbristylis castanea*) are the only conspicuous plants. Near the western edge of the dunes, *Ipomoea pescaprae* var. *emarginata* is mixed with *Croton*, and there are scattered clumps of shrubby wolf-berry (*Lycium carolinianum* var. *quadrifidum*), and mesquite (*Prosopis juliflora*).

The dunes are relatively stabilized on the western side of the island, and there we found moderately dense stands of mesquite trees reaching heights of from eight to 10 feet. Prickly-pear cactus (*Opuntia lindheimeri*) was common in those stands of mesquite, and we saw an occasional yucca tree. A fairly dense ground cover was formed by blanket-flower (*Gaillardia pulchella*), marsh-elder (*Iva* sp.), *Flaveria oppositifolia*, *Enstoma exaltatum*, and *Croton capitatus* var. *albinoides*.

A more open, xeric expression of the mesquite-cactus vegetation occurs on exposed, low clay dunes (see description by Price, 1933) located on alkaline flats bordering the laguna. At the time of our visit, most of the mesquites in these stands were dead or dying, the cactus was abundant, and the ground cover, which was sparse, included drop-seed (*Sporobolus virginicus*), ragweed (*Ambrosia psilostachya*), and *Commicarpus scandens*.

On alkaline flats flooded by hypersaline waters of the laguna following heavy rains, *Batis maritima* is found in the lower areas, but on the slightly elevated areas there is low and almost continuous cover of *Monanthochloë littoralis*, in which can be found *Batis*, *Borrichia fructescens*, *Salicornia* sp., *Iva* sp., and sea-lavender (*Limonium carolinianum*).

Near Third Pass, sea oats (*Uniola paniculata*), evening primrose (*Oenothera* sp.), and cordgrass (*Spartina* sp.) are present on the dunes, and on alkaline flats we collected *Conocarpus erectus*, *Leucaena* sp., and *Cassia fasciculata* var. *ferrisiae*.

Itinerary

We reached Washington Beach from Matamoros on July 6, and drove to a point approximately 33 miles south on the beach, where we made Camp 1 on the east side of large dunes 400 yards from the surf. From this camp we worked the beach and dunes and also visited alkaline flats adjacent to the Laguna Madre. On the afternoon of July 8, we drove south along the beach and established Camp 2 on the south side of the Third Pass, approximately 73 miles south of Washington Beach. We had intended to go farther south but were unable to cross the Fourth Pass, an inlet three miles south of the Third Pass. We left the barrier island on the afternoon of July 10, after driving north from Camp 2 to the mouth of the Rio Grande, 11 miles north of Washington Beach.

Mexican fishermen camped at the Fourth Pass told us that, had we been able to cross the Fourth Pass, it would have been possible to drive south on the beach all the way to La Pesca, a fishing village near the mouth of the Río Soto la Marina, approximately 150 miles south of Washington Beach.

Summary of Previous Work in the Area

The ornithologist H. E. Dresser (1865-1866) worked in southern Texas and at Matamoros, Tamaulipas, in 1863, and on one occasion reached the mouth of the Rio Grande ("Boca Grande"). He did not visit the barrier island or the Laguna Madre de Tamaulipas.

In their extensive travels through México, E. W. Nelson and E. A. Goldman made collections at three localities in the coastal region of Tamaulipas but did not reach the barrier island (Goldman, 1951). Goldman collected at Altamira, near Tampico, from April 2 to 24, 1898, and from May 15 to 20 of the same year both he and Nelson made headquarters at Altamira. Nelson and Goldman also collected in the vicinity of Soto la Marina, 25 miles from the coast, from March 1 to 10, 1902, and, from February 13 to 15, they visited Bagdad, described by Goldman (1951:260) as "a village at very low elevation on the Río Grande about 6 miles above the mouth of the river."

In March, 1950, C. von Wedel and E. R. Hall collected four species of mammals and one bird on the barrier island at Boca Jésus María (Eighth Pass). A report of this work published by Hall (1951) contains descriptions of three new subspecies of mammals from the island.

A few records of birds from the southern end of the barrier island and from other parts of coastal Tamaulipas were reported by Robins, Martin, and Heed (1951). In 1953, R. R. Graber and J. W. Graber made ornithological studies in the vicinity of Tampico and also reached the western edge of the Laguna Madre de Tamaulipas. Several papers on this work have appeared (Graber and Graber, 1954*a*, 1954*b*; Graber, 1955), but a comprehensive account of their observations and specimens was not published. Finally, J. R. Alcorn collected some sandpipers 20 miles southeast of Matamoros, on August 21, 1954, obtaining the first record of the Semipalmated Sandpiper (*Ereunetes pusillus*) in Tamaulipas (Thompson, 1958).

Accounts of Species

Catalogue numbers in the following accounts are those of the Museum of Natural History, The University of Kansas.

Reptiles

Gopherus berlandieri Agassiz: Texas Tortoise.—A pelvic girdle and complete shell with a few attached scutes (63494) were found in stabilized dunes at Camp 1 on July 7, and tracks were seen in the same area. Fragments of two other shells (63493, 63495) were found on sand flats between active dunes at Camp 1.

Holbrookia propinqua propinqua Baird and Girard: Keeled Earless Lizard.—This lizard was abundant on dunes and in pebble-strewn blow-out areas between dunes at Camp 2, but it occurred in smaller numbers in the less stabilized dunes of sparser vegetation at Camp 1. Breeding was in progress at both localities, as evidenced

by the presence of eggs in the oviducts of several females, by the heightened coloration of both sexes, and by mating behavior.

The mating behavior of this species has not been described in the literature, and the following observations, made by Raun at Camp 2 on July 8, may be of interest. A male was seen to circle a female as the latter remained motionless with tail curved upward and to the side, exposing a patch of bright pink-orange color on the ventral surface of the tail. At times the male approached the female from the rear and slightly to the side, biting the dorsal part of her neck and simultaneously attempting to effect intromission. The female several times reacted to this approach by running forward a few steps, thereby freeing her neck from the grasp of the male. When the male did not attempt to approach again, the female appeared to invite copulation by moving in front of him with tail elevated and the colored ventral surface prominently displayed. At the time of copulation, the male mounted from the rear on the right side of the female, grasped her neck, and circled his tail beneath her tail; at the same time the hindquarters of the female were arched upward.

To confirm the presumed sexes of the two individuals under observation, both were collected while in copulation. Examination of the still-coupled specimens showed that both hemipenes of the male were everted and the left one had been inserted.

Apparently the pink-orange subcaudal patch of females is present only in the mating season. It was not present on specimens of this species taken by Raun and Wilks on Padre Island, Texas, in autumn, and it is not mentioned in taxonomic descriptions by Axtell (1954) and Smith (1946).

Measurements of adult specimens in our series indicate that females are of smaller average size than males, and, as previously noted by Smith (1946:132), females of this species have disproportionately shorter tails than do males (Table 1).

Holbrookia propinqua was previously collected on the barrier island by Axtell (1954:31; see also Axtell and Wasserman, 1953:2), who took specimens at Boca Jésus María, at a locality six to seven miles south of Boca Jésus María, and at a point 20 miles east-southeast of Matamoros. Axtell (*loc. cit.*) also lists specimens in the Museum of Zoology, University of Michigan, from Tepehuaje and from one mile north of Miramar Beach (Tampico).

Specimens (56): 3 ♂ ♂ adult, 1 ♂ subadult, 63433-436, Camp 1, July 7. 33 ♂ ♂ adult, 63437-440, 63443-445, 63447, 63448, 63450-

TABLE 1.—MEASUREMENTS IN MILLIMETERS OF ADULT SPECIMENS OF *Holbrookia propinqua* FROM THE BARRIER ISLAND OF TAMAULIPAS

SEX	Number of specimens	Snout-vent length	Tail length	Ratio: snout-vent to tail
Male.....	33	56.0±0.5* (49–62)	77.0±0.7 (69–85)	0.731±0.001 (0.682–0.817)
Female....	14	50.9±0.5 (47–53)	62.2±0.9 (57–68)	0.825±0.001 (0.735–0.877)

* Mean ± standard error; range indicated in parentheses.

456, 63458, 63460, 63462, 63463, 63465-468, 63470-478; 13 ♀ ♀ adult, 63441, 63446, 63449, 63457, 63459, 63469, 63479-485; 6 juv., 63442, 63461, 63464, 63486-488; Camp 2, July 9-July 10.

Cnemidophorus gularis Baird and Girard: Whip-tailed Lizard.—At both camps we found this species in the same general habitat in which *Holbrookia* occurred, but in numbers decidedly fewer than the latter.

Specimens (4): 2 ♀ ♀ adult, 63489, 63490, Camp 1, July 7. 1 ♂ adult, 63491, 1 ♀ adult, 63492, Camp 2, July 9.

We failed to take specimens of snakes on the barrier island, but tracks of snakes were noted on two occasions in dunes near Camp 1; one trail led into a burrow of a kangaroo rat.

Birds

Unless otherwise indicated, specimens taken were not molting. For birds undergoing postnuptial or postjuvenal molt, the degree of advancement of the molt is indicated by recording the number of primaries of the old plumage that have not been dropped. For example, the designation "4 P old" signifies that all primaries except the distal four have been molted.

Table 2 presents results of a strip census of birds along the strand, made by three of us from the moving truck on the morning of July 10. Birds characteristically found on sand near the surf were thus conveniently counted in accurate fashion. Birds not ordinarily found on the strand could not be treated this way; most were considerably less abundant than the eight most numerous species listed in Table 2. Over-all, the numbers of individuals listed are a good index of abundance of the Great Blue Heron and of the common charadriiform birds on the beach in early July. The Black Tern is an excep-

TABLE 2.—BIRDS * RECORDED ALONG 17 MILES OF BEACH † ON THE BARRIER ISLAND OF TAMAULIPAS

SPECIES	Number	Birds per mile
Great Blue Heron	9	0.5
Oyster-catcher	1	0.1
Black-bellied Plover	20	1.2
Wilson Plover	53	3.1
Willet	43	2.5
Sanderling	55	3.2
Laughing Gull	136	8.0
Black Tern	19	1.1
Caspian Tern	82	4.8
Least Tern	221	13.0
Royal Tern	301	17.7
Cabot Tern	122	7.2
	Total: 1062	Total: 62.4

* Common Tern, Forster Tern, and Long-billed Curlew also seen but not counted.

† Between 56 and 73 miles south of Washington Beach, 11:00 to 11:45 a. m., July 10, 1961.

tion, however, and this is discussed in the account of that species on page 327.

Pelecanus erythrorhynchus Gmelin: American White Pelican.—A flock of approximately 300 individuals was seen resting at the edge of the Laguna Madre near Camp 2 on July 9. When disturbed by gunshots, the birds circled high over the laguna and flew to the west. Among bones found on sand flats at Camp 1 are a left tarsometatarsus and a pedal phalanx of an American White Pelican.

Supposedly the only breeding colony of this species on the northern Gulf coast is one in the Laguna Madre near Corpus Christi (Peterson, 1960:8), but the possibility of one or more such colonies existing in northeastern Tamaulipas has been suggested by Amadon and Eckelberry (1955:68) on the basis of their observations of individuals seen soaring near the coast 15 to 20 miles south of Brownsville on April 15 and June 5, 1952. According to Hildebrand (1958:153, and personal communication, August 14, 1961), small

colonies of white pelicans do breed in some years on two small islands, in the Laguna Madre of Tamaulipas, located at 25° 26′ North and 93° 30′ West.

In Veracruz the species is recorded as a winter visitant and transient (Loetscher, 1952:22; Amadon and Eckelberry, 1955:68). Coffey (1960:289) reports the following observations for Veracruz and Tamaulipas: a flock of 52 between Tlacotalpan and Alvarado, May 29, 1951; 80 near Cacaliloa, April 20, 1958; 180 birds north of Alvarado, April 24, 1958; four at Altamira, May 28, 1955; flocks of three, 13, and 37 "south" of Matamoros, May 20, 1951; 72 at Lomas del Real, November 20, 1956.

Pelecanus occidentalis Gmelin: Brown Pelican.—Three individuals flew north over the surf near Camp 1 on July 7, and a lone bird was seen diving into the Gulf a short distance beyond the surf near Camp 2 on July 9. Birds seen by us probably were of the population named *P. o. carolinensis,* which is resident along the Gulf coast (Mexican Check-list, 1950:21).

Phalacrocorax sp.: Cormorant.—From 80 to 100 adult and juvenal cormorants were on the laguna at Camp 2 on July 8 and 9. Probably they were Common Cormorants (*P. olivaceus*), but, because specimens were not taken, we cannot eliminate the possibility that some (or all) were Double-crested Cormorants (*P. auritus*). The former breeds in coastal lowlands of eastern México, whereas the latter is known in eastern México only as a winter visitant and has not been recorded in Tamaulipas (Mexican Check-list, 1950:24).

Fregata magnificens Mathews: Magnificent Man-o'-war Bird.—An observation of a lone bird circling high over the laguna at Camp 2 on July 9 seemingly constitutes the third record of this species in Tamaulipas. Previous records were reported by Robins, Martin, and Heed (1951:336), who found "large numbers" in the Barra Trinidad region (8 miles north of Morón) on April 27 to 29, 1949, and mentioned an immature male taken at Tampico on April 23, 1923; this specimen has been identified by P. Brodkorb as *F. m. rothschildi.*

Ardea herodias Linnaeus: Great Blue Heron.—Our records of this heron are limited to the following observations: four individuals on the beach and seven in the laguna at Camp 1, July 7; one on the beach 52 miles south of Washington Beach, July 8; one 74 miles south of Washington Beach, July 8; two at Third Pass, July 8; 41 standing on mud-flats at the edge of the laguna near Camp 2, July 9; nine on the beach 56 to 73 miles south of Washington Beach, July 10; one on the beach 42 miles south of Washington Beach, July 10.

The status of the Great Blue Heron in coastal Tamaulipas remains to be determined. The subspecies *A. h. wardi* (considered a synonym of *A. h. occidentalis* by Hellmayr and Conover, 1948) is resident and breeds on the Gulf coast of Texas and is to be expected as a resident in Tamaulipas (Mexican Check-list, 1950:27). The species may breed south to Veracruz, where Loetscher (1955:22) reports it is "regular at nearly all seasons, chiefly on the coastal plain"; he records an observation near Tamós on July 1. The subspecies *A. h. herodias* and *A. h. treganzai* winter through much of México and have been recorded in Tamaulipas (Mexican Check-list, 1950:27).

Florida caerulea (Linnaeus): Little Blue Heron.—We saw a white (immature) individual feeding with Reddish Egrets along an inlet at Camp 2 on July 8.

Dichromanassa rufescens rufescens (Gmelin): Reddish Egret.—This egret was recorded only about the inlet at Camp 2, where 15 individuals were feeding, either singly or in small groups, on July 8 and 9. We noted frequent use of the "Open Wing" method of foraging, as described by Meyerriecks (1960:108).

Specimen: ♀ juv., 38899, ovary inactive, 587 gm., Camp 2, July 8. This specimen is referable to the nominate subspecies, which is resident along the Gulf coast. Our record seems to be the first for the species in Tamaulipas.

Leucophoyx thula (Molina): Snowy Egret.—Ten individuals of this species were feeding in association with Reddish Egrets in the inlet at Camp 2 on July 9.

Hydranassa tricolor (P. L. S. Müller): Tricolored Heron.—An observation of one individual flying along the margin of the laguna near Camp 2 is our only record of this species.

Nycticorax nycticorax (Linnaeus): Black-crowned Night Heron.—This heron was found only at the edge of the laguna near Camp 2; ten individuals were noted on July 8, and 20 were seen perched in a clump of mesquite trees on July 9. Perhaps half the birds seen were in juvenal plumage. A juvenile was shot and examined on July 9 but was not preserved as a specimen.

There appears to be no definite evidence of breeding by this species in Tamaulipas (Mexican Check-list, 1950:32), but such may be expected because the species breeds locally in Texas (Peterson, 1960:19) and in Veracruz.

Ajaia ajaja (Linnaeus): Roseate Spoonbill.—On July 9 at Camp

2, 38 spoonbills flew up from the edge of the laguna where they had been resting near a large flock of white pelicans.

Cathartes aura (Linnaeus): Turkey Vulture.—One Turkey Vulture was seen flying east at a point 2 miles west of Washington Beach on July 10. It is noteworthy that we saw no Yellow-headed Vultures (*C. burrovianus*), a species recently recorded in the region of Tampico north to Lomas del Real (Graber and Graber, 1954*a*).

Colinus virginianus texanus (Lawrence): Bob-white.—This species was seen only in or near clumps of mesquite near Camp 1, where three covies (7, 13, and 18 individuals) were flushed on July 7. Specimen: ♂ juv., 38900, testis 3 mm., 100 gm., 6 P old, Camp 1, July 7.

Porzana carolina (Linnaeus): Sora Rail.—On sand flats at Camp 1 we found a left humerus and several other post-cranial skeletal elements that have been identified by Dr. Pierce Brodkorb as belonging to this species. All the bones are of Recent age. We have no other record of the Sora Rail on the barrier island, but in all probability it occurs as a migrant and winter visitant along margins of the laguna.

Haematopus ostralegus Linnaeus: Oyster-catcher.—One individual was seen at Camp 2 on July 8, three were noted at the same locality on July 9, and one was present on the beach 72 miles south of Washington Beach on July 10. The only previous records of this species in Tamaulipas are a specimen (♂, 29348) taken by E. R. Hall 10 miles west and 88 miles south of Matamoros on March 20, 1950 (herewith reported for the first time), and three seen on the beach near Tepehuaje on May 9, 1949 (Robins, Martin, and Heed, 1951).

Squatarola squatarola (Linnaeus): Black-bellied Plover.—Plovers of this species were uncommon but regular on the beach; frequently two individuals were seen together, sometimes in association with one or more Willets. Specimens (4): ♂, 38915, testis 4 mm., 231 gm.; ♂, 38914, testis 4 mm., 221 gm.; ♂, 38916, testis 3 mm., 209 gm., Camp 1, July 7. Male, 38917, testis 4 mm., 186 gm., Camp 2, July 9. The specimens were molting (3-4 P old) into winter plumage and showed little or no subcutaneous fat.

Our specimens and records probably pertain to nonbreeding individuals summering on the coast, as the species is known to do in Texas (Hagar and Packard, 1952:9) and elsewhere in its range (Eisenmann, 1951:182; Haverschmidt, 1955:336; A.O.U. Check-list,

1957:174). In any event, our dates (July 6 to 10) are unusually early for autumnal migrants; they do not reach Texas until August (Peterson, 1960:94), and Loetscher (1955:26) gives August 7 as the earliest date for southbound migrants in Veracruz.

Charadrius hiaticula semipalmatus Bonaparte: Ringed Plover.—We have a single record, an adult male (38913, testis 2 x 1 mm., heavy fat, 47.0 gm., 4 P old) taken on a sandbar at Camp 2 on July 9. The bird was feeding in company with a flock of Sanderlings.

There is no previous record of the Ringed Plover in Tamaulipas. In Texas, Hagar and Packard (1952:8) indicate that the first autumnal migrants reach the central Gulf coast in the last week of July. In coastal México, the species has previously been recorded from August 23 to May 12 (Mexican Check-list, 1950:91). Therefore, the present record must represent an exceptionally early southbound migrant, or, more probably, a nonbreeding, summering individual. According to the A.O.U. Check-list (1957:166), nonbreeding birds are found in summer in coastal areas south to California, Panamá, and Florida. Many individuals spend the northern summer along the coast of Surinam (Haverschmidt, 1955:336).

Charadrius wilsonia wilsonia Ord: Wilson Plover.—This small plover breeds commonly on the beach and on alkaline flats adjacent to the laguna. Previous evidence of breeding in Tamaulipas consisted only of a report of a male with brood patches and an enlarged testis taken near Tamós on May 30, 1947 (Loetscher, 1955:26).

We saw many pairs of adults and a large number of well-grown juveniles, and, at a point 4 miles south of Washington Beach, we collected a brood of three small juveniles that had only recently hatched. The breeding season apparently was drawing to a close, for several adults in our collection were in postnuptial molt and showed marked gonadal regression. From July 6 to 9, a few small groups of birds were noted, but large groups were not seen until July 10, when several flocks of up to 60 individuals were found along the coast 3 to 7 miles south of Washington Beach.

Specimens (12): ♂, 38904, testis 4.5 x 2 mm., 58 gm., 3 P old, brood patches refeathering; ♂, 38905, testis 5 x 2 mm., 59 gm., 4 P old, brood patches refeathering; ♂ juv., 38903, 6.2 gm.; 2 sex?, 38901, 38902, 5.7 and 6.2 gm., 4 miles south of Washington Beach, July 6. Male, 38907, testis 5 x 2 mm., 56 gm., 7 P old, brood patches refeathering; ♀, 38906, ova to 1 mm., 61 gm., 3 P old, brood patches refeathering; ♀ juv., 38908, ovary inactive, 54 gm., in body molt; Camp 1, July 6. Male, 38910, testis 6 x 3 mm., 60 gm., 4 P old; ♀,

38909, ova to 1 mm., 57 gm., 4 P old, brood patches refeathering; Camp 1, July 8. Male, 38911, testis 2 x 1 mm., 55 gm.; juv., 38912, no weight or sex recorded; Camp 2, July 9.

Numenius americanus parvus Bishop: Long-billed Curlew.—Lone individuals and groups of two to five were noted occasionally along the beach each day. In total, some 30 to 50 birds were counted, but some individuals may have been recorded more than once on different days. Specimens (2): ♂, 38918, testis 4 mm., some fat, 459 gm., Camp 2, July 9; ♀, 38933, ova to 1 mm., no weight recorded, Camp 2, July 8.

Our assumption that some or all individuals seen by us were nonbreeding, summering birds is supported by the fact that our specimens are referable to the small, northwestern subspecies, *N. a. parvus,* rather than to *N. a. americanus;* the latter breeds south in the eastern United States to south-central Texas (A.O.U. Check-list, 1957:181). Loetscher (1955:27) saw a flock of 39 curlews near Tamós on June 30, and he notes that nonbreeding birds are fairly common at all seasons in Veracruz. Similarly, the species is present throughout the year on the central Gulf coast of Texas (Hagar and Packard, 1952:8). Authors of the Mexican Check-list (1950:94) do not mention the possibility that birds of this species recorded in México in July are summering rather than migrating. Twelve supposed migrants seen along Laguna Chila (Cacalilao), Veracruz, by Coffey (1960:291) on May 31, 1957, may have been summering birds.

Limosa fedoa (Linnaeus): Marbled Godwit.—Three were seen in shallow waters of the laguna at Camp 2 on July 9. Specimen: ♂, 38919, testis 6 x 2 mm., fat, 305 gm., 6 P old, Camp 2, July 9. Probably our records were of nonbreeding birds, which are known to occur in summer elsewhere in México (Mexican Check-list, 1950: 94), sparingly in Texas (Hagar and Packard, 1952:8), and in South Carolina (A.O.U. Check-list, 1957:205). Apparently the only record for this species in Veracruz is one seen on May 11, 1954, east of Cacalilao (Coffey, 1960:292).

Tringa melanoleuca (Gmelin): Greater Yellowlegs.—Three birds were seen on alkaline flats at Camp 1 on July 7, and two were noted at Camp 2 on July 9. There is one previous report of this species in Tamaulipas, and, since it has been recorded as a migrant and winter resident in México between July 26 and April 26 (Mexican Check-list, 1950:95), our records seem to pertain to unusually early autumnal migrants or, possibly, to nonbreeding, summering

birds. Other mid-summer records are available from Tamós on June 30 and July 1, and the species is "to be expected every month of the year" in Veracruz (Loetscher, 1955:27). Sight records for Veracruz in May (Coffey, 1960:291) may well pertain to summering birds. There are northern-summer records for this species from Texas (Hagar and Packard, 1952:8), Surinam (Haverschmidt, 1955: 367), and other areas within the winter range of this yellowlegs (A.O.U. Check-list, 1957:190).

Catoptrophorus semipalmatus semipalmatus Gmelin: Willet.— The Willet was common on the island. We found evidence of breeding and also saw large flocks of birds that were either nonbreeders summering in the area or early, postbreeding migrants from more northerly places. All along the beach and at the edge of the laguna at both camps we found Willets in twos or threes, often accompanied by one or two Black-bellied Plovers. On July 10 a small juvenile was captured; two adults in breeding plumage evidenced obvious concern at this action. On July 6 a flock of 30 birds flew east over Camp 1, and a flock of 90 was seen flying south over Camp 1 on July 7.

Specimens (7): ♂, 38922, testis 6 x 1 mm., 264 gm., breeding plumage; ♀, 38923, ova to 2 mm., 269 gm., breeding plumage; ♀, 38924, ova to 1 mm., 280 gm., 3 P old; ♀, 38925, ova to 1 mm., 319 gm.; ♂, 38921, testis 7 x 2 mm., 211 gm., breeding plumage; Camp 1, July 7. Male, 38927, fat light, 231 gm., 4 P old, Camp 2, July 9. Juvenile, sex not recorded, 38920, 43.0 gm., 1 mile south of Washington Beach, July 10. Two of our specimens, both males, are in worn breeding plumage and evidence no molt; another specimen, a female, is also in breeding plumage but is molting on the breast. The remaining two adult skins in our series are three-quarters through the molt and are for the most part in fresh winter feather.

Dresser (1866:37) took an unspecified number of specimens of the Willet at the "Boca Grande" in July and August, but actual breeding in Tamaulipas was first established by C. R. Robins, who found a "scattered colony of breeding Willets" and took a female with an egg in the oviduct on May 9, 1949, near Tepehuaje (Sutton, 1950:135). Sutton (*op. cit.*) has discussed the characters of this specimen and of birds from Cameron County, Texas. The specimen from Tepehuaje reportedly is closer to *C. s. inornatus* than to *C. s. semipalmatus* both in size and color, and birds from Cameron County are intermediate between the two subspecies in size but like *C. s. inornatus* in color.

Measurements of our five adults from the barrier island are presented in Table 3 for comparison with those of *C. s. semipalmatus* and *C. s. inornatus* given by Ridgway (1919:316-319). Like the

TABLE 3.—MEASUREMENTS IN MILLIMETERS OF SPECIMENS OF CATOPTROPHORUS SEMIPALMATUS FROM THE BARRIER ISLAND OF TAMAULIPAS

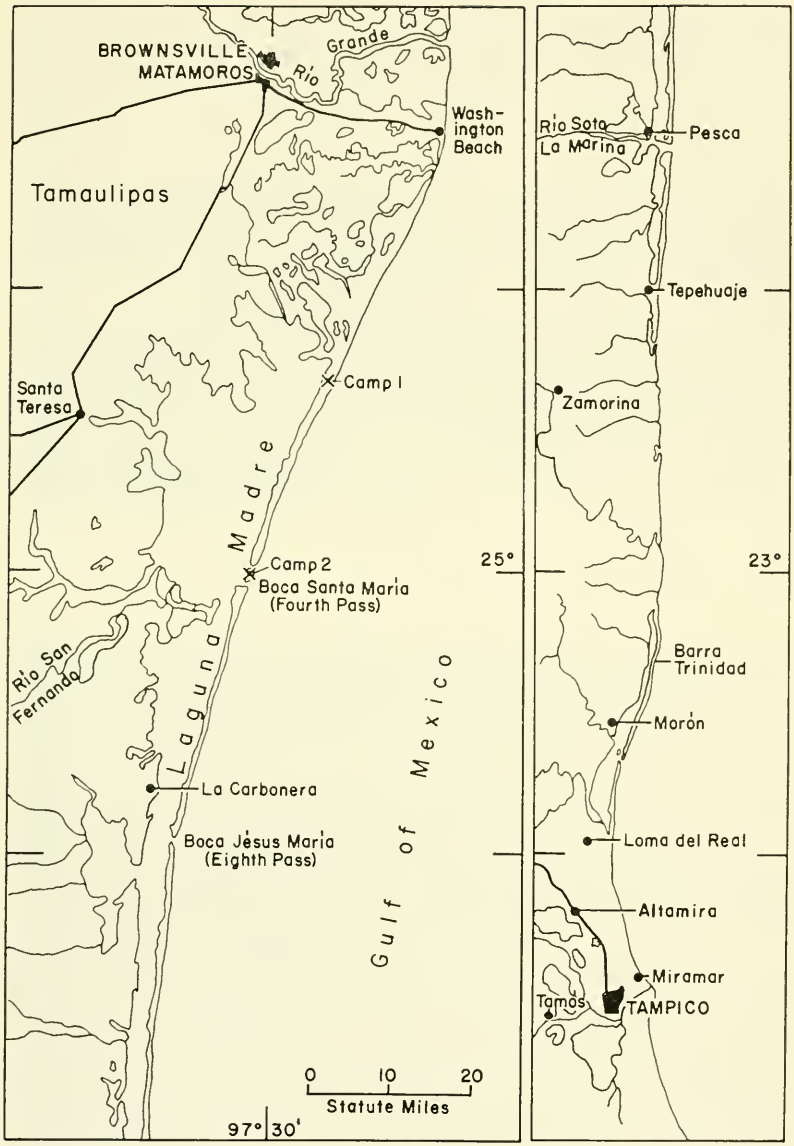
SEX AND CATALOGUE NUMBER	Wing	Tail	Full culmen	Tarsus	Weight in grams
♂ 38921*.....	197	80.6	61.0	59.0	211
♂ 38922*.....	198	74.4	61.9	57.9	264
♂ 38927.....	194	75.5	60.4	56.4	231
♀ 38923*.....	201	71.0	59.0	55.4	269
♀ 38924.....	199	71.0	61.3	59.0	280

* Specimens in worn breeding plumage.

specimens from Cameron County examined by Sutton (*op. cit.*), our birds are intermediate in size between average-sized individuals of the two named subspecies. In color and pattern, we find that our specimens in breeding plumage fall within the range of variation of *C. s. semipalmatus* as exemplified by five specimens in nearly identical states of wear and fading in the Museum of Natural History.

On the basis of the evidence presently available, we are reluctant to follow Sutton (1950:136) in assigning breeding birds from the Gulf coastal region to *C. s. inornatus,* a name otherwise applied to a population of birds breeding inland, in northwestern North America south to central Utah and Colorado and east to South Dakota (and formerly to western and southeastern Minnesota and Iowa; see A.O.U. Check-list, 1957:190). The intermediate characters of birds breeding in coastal Texas and Tamaulipas probably represent not the results of actual genetic intermixing of the two named populations but, rather, an adaptive response of the eastern coastal stock (*C. s. semipalmatus*) to environmental modalities distinct from those operating elsewhere within the range of the eastern coastal population or on the inland population. Accordingly, we tentatively use the name *C. s. semipalmatus* for our Tamaulipan specimens, realizing that the patterns of geographic variation in the species do not lend themselves well to taxonomic treatment by the trinomial no-

PLATE 5



Map of coastal Tamaulipas, showing the barrier island and localities mentioned in text. Stippled areas are extensively marshy.

FIG. 1.—*Croton* and *Fimbristylis* on stabilized dunes; the Laguna Madre and surrounding alkaline flats and clay dunes are visible in the background. Habitat of Road-runner, Ord kangaroo rat, and keeled lizard.

FIG. 2.—Active dune near Camp 1. Other active dunes can be seen in the background, in the right foreground is a clump of *Croton*, and in the left foreground is a small clump of *Fimbristylis*. Habitat of Road-runner, Ord kangaroo rat, and keeled lizard.

menclatural system. The need for a comprehensive analysis of geographic variation in this species, based, if possible, on proper segregation of age classes along the lines followed by Pitelka (1950) for *Limnodromus,* is obviously indicated.

Arenaria interpres morinella (Linnaeus): Turnstone.—Approximately 40 individuals were noted along the beach from July 6 to 10, mostly in small groups; the largest flock included 15 individuals. Specimens (5): ♂, 38931, testis 4 x 1 mm., moderately fat, 107 gm., 4 P old; ♂, 38932, testis 3 x 1 mm., moderately fat, 103 gm., molting; 75 miles south of Washington Beach, July 8. Male, 38928, testis 2 mm., 111 gm., 3 P old; ♂, 38929, testis 3 mm., moderately fat, 106 gm., 6 P old; ♂, 38930, testis 2.5 mm., moderately fat, 108 gm., 6 P old; Camp 2, July 9.

The only previous record of the Turnstone in Tamaulipas is an observation of an unspecified number at Tepehuaje on May 9, 1949 (Robins, Martin, and Heed, 1951). The dates of our records suggest that nonbreeding birds summer along the coast of Tamaulipas. The species is present in small numbers in summer along the central Gulf coast of Texas (Hagar and Packard, 1952:8). Loetscher (1955: 26-27) does not report records for Veracruz in summer, but records of the species in Yucatán on May 31, 1952 (Paynter, 1955:101), and on June 16, 1900 (Mexican Check-list, 1950:79), probably represent summering nonbreeders. Probably also in the same class are supposed "migrants" seen at Coatzacoalcos on May 17, 1954, and June 4, 1955 (Coffey, 1960:290).

Inasmuch as Haverschmidt (1955:368) reports that nonbreeding birds summering in Surinam only occasionally assume breeding plumage, it is noteworthy that our specimens were molting from nuptial (summer) to winter plumage. None of the nonbreeding northern shorebirds observed by Eisenmann (1951:183) in Panamá in summer were in nuptial plumage.

Crocethia alba (Pallas): Sanderling.—This sandpiper was noted each day along the beach, occasionally singly but more frequently in groups ranging from 10 to 50 individuals. Specimens (7): ♂, 38936, testis 2 mm., light fat, 49 gm., 5 P old, Camp 1, July 7. Female, 38937, ova to 1 mm., fat, 58 gm., 4 P old; ♂, 38939, fat, no weight recorded, 6 P old, breeding plumage; 3 ♂ ♂, 38940-38942, fat, no weight recorded, 4-5 P old; Camp 2, July 9.

With one exception as noted, our specimens are in worn, nonbreeding plumage and are replacing their old feathers with new ones fundamentally the same in color and pattern; the exceptional

specimen is molting from worn breeding plumage into nonbreeding plumage. Only one other individual in breeding feather was seen on the island.

According to the Mexican Check-list (1950:99), the Sanderling has been recorded in México from August to May 19. In Texas, Peterson (1960:107) reports that it is a migrant, April to June and July to November, and that it winters along the coast. We suspect that many of the birds present in Texas in June and July, together with those recorded by us in Tamaulipas in July, are nonbreeding, summering individuals. Haverschmidt (1955:368) reports northern-summer records from Surinam, and, according to the A.O.U. Check-list (1957:208), nonbreeding birds occur in summer extensively through winter range of the species, including the Gulf coast of the United States.

Micropalama himantopus (Bonaparte): Stilt Sandpiper.—Two birds in worn winter plumage were taken as they foraged together at the edge of the laguna near Camp 2 on July 9. Specimens (2): ♂, 38934, testis 2.5 mm., heavy fat, 116 gm., 4 P old; ♂, 38935, testis 3 mm., fat, 111 gm., 4 P old.

Our specimens probably were nonbreeding birds summering between the breeding range in arctic America and the winter range in northern South America. The A.O.U. Check-list (1957:202) does not mention nonbreeding, summering records of this species. The 251 birds seen by Coffey (1960:292) at Cacalilao, Veracruz, on May 11, 1954, were probably migrants.

Recurvirostra americana Gmelin: American Avocet.—This species was seen only in three large flocks flying south along the beach, as follows: 56 birds 72 miles south of Washington Beach, July 8; 38 birds 73 miles south of Washington Beach, July 8; 29 birds 72 miles south of Washington Beach, July 10. All birds were in winter plumage.

All these birds were possibly autumnal migrants, but the dates are early; the species has not previously been recorded on migration in México before August (Mexican Check-list, 1950:101). The species is known to breed in San Luis Potosí (Mexican Check-list, *loc. cit.*) and along the lower coast of Texas ("rarely to Brownsville"; A.O.U. Check-list, 1957:209); avocets thus may also breed in coastal Tamaulipas.

Larus argentatus Pontoppidan: Herring Gull.—A first-year bird was observed near Camp 2 on July 8, and two subadult individuals

were seen on the beach between the Third and Fourth passes on July 8.

Larus atricilla Linnaeus: Laughing Gull.—This gull was common all along the beach. Many individuals were in full breeding feather and many subadult birds were also present. Specimens (6): ♂ subadult, 38944, testis 5 x 1 mm., 325 gm., molting; ♀, 38945, ovary small, 309 gm., in molt, brood patches refeathering; sex?, 38943, 315 gm., in molt; sex? subadult, 38946, 327 gm., in molt; Camp 1, July 7. Female subadult (second-year), 38947, 305 gm., in molt, Camp 2, July 8. Female, 38926, ova to 2.5 mm., 313 gm., 8 P old, Camp 2, July 10.

The Mexican Check-list (1950:105) refers to the Laughing Gull as a common winter resident on both coasts of México from August 7 to May 17, but Loetscher (1955:29) found it locally common throughout the year on the coast of Veracruz, and he mentioned seeing birds a short distance south of Tampico in June and July. The status of this gull in Tamaulipas remains to be determined; probably it will be found breeding locally, but many of the birds summering in eastern México are most likely nonbreeders (A.O.U. Check-list, 1957:226).

Chlidonias niger surinamensis (Gmelin): Black Tern.—On July 6, 7, 8, 9, and on the morning of July 10, we saw this species only occasionally, recording in total not more than 50 individuals. But, about noon on July 10, we observed at least 300 birds in compact flocks of about 50 individuals each between Washington Beach and a point about 9 miles south of that locality. Approximately one in ten birds seen was in breeding plumage, the rest being in winter or subadult plumages, which are indistinguishable in the field. Perhaps some of the birds seen were nonbreeding, summering individuals, but we presume that the large groups were southbound migrants, and we note that autumnal migrants appear in northern Veracruz as early as July 1 (Loetscher, 1955:30). On the central Gulf coast of Texas, Hagar and Packard (1952:9) indicate that an influx of birds occurs in the last week of July, and small numbers of birds, presumably nonbreeding individuals, are present along the Gulf coast throughout June and July. Dresser (1866:45) found this species to be "common at the Boca Grande during the summer."

Specimens (2): ♂, 38948, testis 6 mm., moderately fat, 68 gm., in breeding plumage, Camp 1, July 7. Female, 38949, ovary inactive, 49 gm., molt into winter feather almost complete, Camp 2, July 10.

Hydroprogne caspia (Pallas): Caspian Tern.—The only published record of the Caspian Tern in Tamaulipas is a report of one seen at Lomas del Real on November 20, 1956 (Coffey, 1960:260), but we found it moderately common all along the beach and at the margin of the laguna. It was frequently associated with the Royal Tern, which outnumbered it better than three to one (see Table 2). The species is resident and breeds along the coast of Texas, and it probably has similar status in Tamaulipas. However, in Veracruz it is known only as a winter visitant (Loetscher, 1955:30) and as a spring migrant (Coffey, 1960:293). Specimen: ♀, 38950, ova to 2 mm., moderately fat, weight not recorded, 5 P old, Camp 2, July 9.

Sterna hirundo hirundo Linnaeus: Common Tern.—We took a specimen (♂ ?, 38951, no fat, 165 gm.), 49 miles south of Washington Beach on July 8, and saw two others over the laguna at Camp 2 on July 9. Our specimen had nearly finished with molt and feather growth into adult winter plumage. The status of Common Terns in Tamaulipas is uncertain; our record, and records from Tamós on July 1, 1952, and June 12, 1953 (Loetscher, 1955:29), probably pertain to nonbreeding, summering birds. Yet, the species has bred on the Texas Gulf coast (A.O.U. Check-list, 1957:235), and it reasonably may be expected to nest in Tamaulipas. Coffey (1960:293) saw two individuals at Altamira on May 10, 1954.

Sterna forsteri Nuttall: Forster Tern.—Six were recorded near Camp 1 on July 7, and two were seen on the beach on July 6 and 10. The Mexican Check-list (1950:108) does not cite records for Tamaulipas, but the A.O.U. Check-list (1957:234) includes northern Tamaulipas within the breeding range. Evidence suggesting breeding of the species in extreme northern Veracruz is reported by Loetscher (1955:29) in the form of a female specimen with "ovary greatly enlarged" taken seven miles west of Tampico on May 30, 1947. In the same area the species also seems to spend the summer as a nonbreeder, for Loetscher (*loc. cit.*) saw 20, nearly all in nonbreeding plumage, on July 1, 1952.

Specimens (4): ♂, 38952, testis 4.5 mm., 150 gm., 8 P old; ♂, 38955, testis 2 mm., 138 gm., 2 P old; ♂, 38953, testis 5 x 1 mm., 142 gm., 5 P old; ♀, 38954, ova to 1 mm., 148 gm., 2 P old; Camp 1, July 7.

Sterna albifrons antillarum (Lesson): Least Tern.—The status of this species in Tamaulipas is uncertain, but there is reason to

believe that it breeds, at least in small numbers. We found the species moderately common and generally flying about in twos, possibly mated pairs, near both camps and on the beach. Breeding is suggested by the large sizes of the testes of the two males collected and by the presence of brood patches on a female taken on July 6, but we have no direct evidence of nesting in Tamaulipas, and it should be noted that this species is known to spend the summer in nonbreeding condition at many places (A.O.U. Check-list, 1957: 239). Loetscher (1955:30) suggests that the species may be found breeding in Veracruz and mentions a record of 15 seen at Miramar, Tamaulipas, on June 26, 1952. Dresser (1866:45) found it to be "abundant" at the "Boca Grande" in summer.

On July 10, we saw flocks of 15 to 20 individuals flying along the beach a few miles south of Washington Beach.

Specimens (4): ♂, 38958, testis 11 x 4 mm. (right testis 5 x 4 mm.), light fat, 45 gm., 6 P old; ♂, 38959, testis 11 x 4 mm. (right testis 7 x 4 mm.), light fat, 45 gm., 6 P old; ♀, 38956, ova to 2.5 mm., 42.5 gm., 6 P old, brood patches refeathering; Camp 1, July 6. Female, 38957, ova to 1 mm., 44 gm., Camp 1, July 7. This last specimen had essentially completed the autumnal molt into winter plumage, with only a few feathers remaining ensheathed basally.

Our specimens are referable to *S. a. antillarum,* being paler dorsally and slightly lighter gray on the hind-neck than specimens of *S. a. athalassos* from Kansas, with which they were compared.

Thalasseus maximus maximus (Boddaert): Royal Tern.—This species was common all along the beach, occurring for the most part in flocks of from ten to 50 individuals in association with Cabot Terns. Data on gonadal condition and brood patches of some of our specimens suggest that breeding occurs in coastal Tamaulipas, as previously reported by the Mexican Check-list (1950:110). Robins, Martin, and Heed (1951) report seeing one Royal Tern near Tepehuaje on May 9, 1949, and Dresser (1866:44) found the species "common at the Boca del Rio Grande during the summer."

Specimens (6): ♂, 38960, testis 9 x 4.5 mm., not fat, 484 gm., 6 P old, brood patches refeathering, 4 miles south of Washington Beach, July 6. Male, 38961, testis 7 x 3 mm., 455 gm., no brood patches, 8 miles south of Washington Beach, July 6. Male, 38962, testis 10 x 5 mm., 387 gm., brood patches refeathering; ♀, 38963, ova to 1 mm., 358 gm., 3 P old; ♀, 38964, ova to 3 mm., 389 gm., 8 P old; Camp 1, July 7. Female, 38994, ova to 2 mm., 536 gm., brood patches refeathering, Camp 2, July 10.

Thalasseus sandvicensis acuflavidus (Cabot): Cabot Tern.—This tern was moderately common along the beach and margin of the laguna, and it was seen frequently in company with Royal Terns. Like the latter, this tern breeds in coastal Texas (A.O.U. Check-list, 1957:241), and it probably also nests in Tamaulipas, although direct evidence is not available. The only previous record of this species in Tamaulipas is a report (Robins, Martin, and Heed, 1951) of two observed on the beach near Tepehuaje on May 9, 1949.

Specimens (4): ♂, 38965, testis 9 x 4.5 mm., 208 gm., 9 P old, 49 miles south of Washington Beach, July 8. Male, 38966, testis 8 x 3 mm., not fat, 192 gm., 8 P old; ♀, 38967, ova to 3 mm., 193 gm., 7 P old, brood patches refeathering; ♀, 38968, ova to 1 mm., 186 gm., 8 P old, no brood patches; 52 miles south of Washington Beach, July 8.

Rynchops nigra nigra Linnaeus: Black Skimmer.—We found this species moderately common at the edge of the laguna at both camps and occasionally saw it along the beach. Generally two birds, probably mated pairs, were seen together; twice birds were seen carrying food in their bills, presumably intended for nestlings. The species is known to nest in Tamaulipas from "Matamoros Lagoon" south to Tampico (Mexican Check-list, 1950:112).

Specimens (2): ♂, 38970, testis 40 x 23 mm. (abnormally large, possibly as a result of hemorrhage), 418 gm., brood patches refeathering; ♂, 38969, testis 17 x 4 mm., fat light, 442 gm., brood patches refeathering; Camp 1, July 7.

Zenaidura macroura Linnaeus: Mourning Dove.—Our only record is a lone bird seen in a mesquite near Camp 1 on July 6. Possibly the species breeds along the margin of the laguna, although Aldrich and Duvall (1958:113, map) do not include coastal Tamaulipas in the known breeding range. Loetscher (1955:30) suggests that the Mourning Dove may be found breeding in the lowlands of northern Veracruz and cites a record of one seen at Tamós on July 1, 1952.

Geococcyx californianus (Lesson): Road-runner.—At least four individuals were seen in large dunes at Camp 1 on July 7 and 8. On several occasions we watched them pursue lizards (*Holbrookia propinqua*) at the margins of clumps of *Croton* and *Ipomoea*.

Chordeiles minor aserriensis Cherrie: Nighthawk.—Nighthawks of this species were seen regularly at Camp 1, where we flushed them from alkaline flats in the day and heard them calling as they foraged over the dunes in late afternoon.

Specimens (3): ♂, 38971, testis 5 mm., no fat, 62 gm., Camp 1, July 6. Male, 38972, testis 7.5 mm., no fat, 58 gm.; ♂, 38973, testis ?, no fat, 53 gm.; Camp 1, July 7. The gonads of these birds were not in full breeding condition, but it is highly probable that the birds were members of a population that had bred in the area.

Variation in *Chordeiles minor* in Tamaulipas has recently been studied by Graber (1955). Two specimens taken by him on August 3, 1953, approximately 9 miles south of Carbonera, resemble birds from Terrell County, Texas, and represent *C. m. aserriensis,* as do our three birds from the barrier island. Two of Graber's specimens from Lomas del Real, in southeastern Tamaulipas, are distinctly darker and probably represent *C. m. neotropicalis,* a subspecies subsequently described from Chiapas (Selander and Alvarez del Toro, 1955).

Muscivora forficata (Gmelin): Scissor-tailed Flycatcher.—On July 7 near Camp 1, two individuals were found in stands of mesquite. One was taken and proved to be an adult male (38974, testis 6 x 3 mm., not fat, 40 gm.) in postnuptial molt (6 P old).

We presume that the two birds recorded by us were members of a population breeding on the barrier island, rather than autumnal migrants. The Mexican Check-list (1957:69) records this species in México only as a transient and winter visitant. But, on the basis of records of birds seen along the highway between Matamoros and Ciudad Victoria, Davis (1950) has suggested that the species breeds in Tamaulipas, and this is supported by a report of one seen at the north end of the Monterrey Airport on June 1, 1957 (Coffey, 1960: 294). Brown (1958) has recently established that the species breeds in Nuevo León by finding a nest 33 kilometers (by road) north of Sabinas, Hidalgo, on July 19, 1954.

Myiarchus cinerascens cinerascens (Lawrence): Ash-throated Flycatcher.—A juvenal male (38975, testis 2 mm., no fat, 35.0 gm.) taken in mesquite at Camp 1 constitutes our only record for this species. Lanyon (1961:441, map) has shown that most of Tamaulipas is devoid of these flycatchers in the breeding season; the nearest known breeding Ash-throated Flycatchers are slightly west of Corpus Christi, Texas, about 200 miles north-northwest of Camp 1 on the barrier beach. Our specimen closely resembles eight specimens from Coahuila, México, in general coloration and, especially, in the pattern of colors on the outer rectrices. Probably No. 38975 was from southwestern Texas or Coahuila and had begun its southward migration. Against this idea lies chiefly the fact that young-

of-the-year tend to move south later than adults of the same species; so, this bird possibly had been reared in coastal Tamaulipas.

Eremophila alpestris giraudi (Henshaw): Horned Lark.—This species occurred in moderate numbers on alkaline flats and almost barren sand flats at both camps. At the time of our visit to the island, the breeding season apparently was coming to an end, but we noted no tendency in the birds to flock.

Specimens (7): ♂, 38981, testis 6 mm., 21.0 gm.; ♂, 38977, testis 7.5 x 4 mm., not fat, 27.5 gm.; ♂, 38979, testis 11 x 7 mm., 29.0 gm.; ♀, 38976, ova to 3 mm., brood patch vascular but regressing, no fat, 24.4 gm.; sex? juv., 38987, no fat, 21.0 gm.; sex? juv., 38980, 24.0 gm.; Camp 1, July 7. Male, 38982, testis 9.5 x 6 mm., 27.5 gm., Camp 2, July 9.

The subspecies *E. a. giraudi,* which is endemic to the Gulf coastal plain of Texas and Tamaulipas, has been reported in Tamaulipas previously only from Bagdad, near Matamoros (Mexican Check-list, 1957:106). The fact that our specimens show characters totally consistent with those of *E. a. giraudi* indicates that there is little genetic interchange between the population we sampled and those of *E. a. diaphora,* the closest of which reportedly breeds at Miquihana, in southwestern Tamaulipas.

Corvus cryptoleucus Couch: White-necked Raven.—Several groups of six to ten birds were present at Washington Beach on July 6 and 10; but, southward on the island, we recorded this species only once, on July 9, when a lone individual flew near Camp 2, being pursued and "buzzed" by two Least Terns. The Mexican Crow (*Corvus imparatus*) reportedly is common in the coastal region of Tamaulipas (Mexican Check-list, 1957:118) but was not seen by us.

Thryomanes bewickii cryptus Oberholser: Bewick Wren.—This species seemingly breeds in small numbers in mesquite stands near Camp 1, where we obtained a juvenile and saw another individual. Specimen: ♀ juv., 38983, no fat, 10.0 gm., Camp 1, July 8. *T. b. cryptus* is reported to intergrade with *T. b. murinus* of Veracruz in southern Tamaulipas (Mexican Check-list, 1957:160-161).

Mimus polyglottos leucopterus (Vigors): Northern Mockingbird. —We recorded this species only near Camp 1, where a few pairs were breeding in stands of mesquite. Males were in full song and territorial display.

Specimens (2): ♂, 38985, testis 11 x 7 mm., not fat, 43 gm.; ♀, 38984, ova to 4.5 mm., vascular brood patch, 49.0 gm.; Camp 1, July 7.

PLATE 7

FIG. 1.—Mesquite-cactus formation on clay dune at margin of the Laguna Madre west of Camp 1. Habitat of Northern Mockingbird, Cardinal, Bob-white, black-tailed jackrabbit, and Great Plains woodrat.

FIG. 2.—*Batis-Monanthochloë* formation on alkaline flats near the Laguna Madre, with mesquite bordering stabilized dunes in the left background. *Salicornia*, a classical dominant of salt marshes, is here relatively inconspicuous. Habitat of Nighthawk and Horned Lark.

PLATE 8

"Fossilized" burrow of Texas Pocket Gopher in a sandy trough between active dunes. A part of the cast has been broken away to show the general shape of the old burrow. The diameter of the cast is about 3.5 inches.

Cassidix mexicanus prosopidicola Lowery: Great-tailed Grackle. —Small, postbreeding flocks composed of both adult and juvenal birds were seen moving along the edge of the laguna at Camp 1. In the morning the flocks flew south, and in the afternoon groups of similar size flew north, presumably to a roost at an undetermined distance north of our camp. Occasionally, a few birds stopped to rest or to forage on the dunes or in stands of mesquite. At Camp 2 on July 9, a postbreeding adult female and a well-grown, presumably independent juvenile were taken as they perched in a clump of mesquite in which we found three old nests of *Cassidix;* two of the nests were about four feet apart in one tree, and the third was in another tree 100 feet from the first.

Specimens (4): ♂ adult, 38988, testis 6 mm., no fat, 209 gm., 6 P old, Camp 1, July 7. Female, 38989, ova to 3 mm., fat, 115 gm., old brood patch, Camp 1, July 8. Female, 38990, ova to 1 mm., moderate fat, 107 gm., 7 P old, brood patch refeathering; ♂ juv., 38991, testis 3 x 1 mm., not fat, 172 gm., 6 P old; Camp 2, July 9.

Specimens from the barrier island are clearly referable to *C. m. prosopidicola,* showing no approach to the larger and, in the female,

TABLE 4.—MEASUREMENTS IN MILLIMETERS OF ADULT MALES OF CASSIDIX MEXICANUS

LOCALITY	No.	Wing	Tail	Tarsus	Weight in grams
Austin, Texas	17–137 [1]	184.3 (173–200)	203.8 (178–232)	46.38 (41.8–50.0)	225.6 June (204–253) 202.2 July (195–207)
San Patricio Co., Texas [2]	5	185.2 (182–188)	204.2 (190–219)	46.74 (45.1–50.2)	237.6 (228–245)
Barrier Is., Tamps.	1	178	185	47.1	209
Victoria, Tamps. [3]	4	192.2 (186–200)	224.2 (215–232)	47.77 (46.0–49.1)	254.3 (239–276)
Tampico, Tamps. [4]	1	197	214	48.3	260
Catemaco, Veracruz [5]	1	193	216	48.2	257

1. Data from Selander (1958: 370, 373). Sample sizes, as follows: wing, 137; tail, 119; bill length, 20 (June and July); tarsus, 133; weight, 17 for June, 3 for July.
2. June 13, 1961; breeding condition.
3. May 6, 1961; breeding condition.
4. May 7, 1961; breeding condition.
5. November 28, 1959.

darker *C. m. mexicanus* of Veracruz and San Luis Potosí. In Table 4, measurements of the adult male from the barrier island may be compared with those of specimens of *C. m. prosopidicola* from Texas and a specimen of *C. m. mexicanus* from Veracruz; it is apparent that our specimen is assignable to the former.

Evidence of intergradation between the two subspecies is shown in a series of birds collected near Ciudad Victoria, Tamaulipas, in May, 1961. The females in the series are highly variable in color individually, but are on the average paler than *C. m. mexicanus* from Veracruz; the males are distinctly larger than *C. m. prosopidicola* from Texas. At Miramar, near Tampico, Tamaulipas, a decided approach to *C. m. mexicanus* is also evident in the dark color of females and in the large size of both males (Table 4) and females.

Agelaius phoeniceus megapotamus Oberholser: Red-winged Blackbird.—This species was recorded only at Camp 1 on July 7, when we saw two males, one of which was flying south along the edge of the dunes in a flock of five Great-tailed Grackles. Specimen: ♂, 38992, testis 10 x 7 mm., fat, 54 gm., Camp 1, July 7. The large size of the testes of this individual indicates breeding condition.

Sturnella magna hoopesi Stone: Eastern Meadowlark.—Meadowlarks were found in small numbers along the margins of the alkaline flats at both camps. Breeding was still in progress, for males were singing and a female shot on July 9 had only recently laid eggs. Specimens (2): ♂, 38986, testis 13 x 8 mm., not fat, 102 gm.; ♀, 38987, ova to 6 mm., 3 collapsed follicles, not fat, 88 gm.; Camp 2, July 9.

Richmondena cardinalis canicaudus Chapman: Cardinal.—This species was recorded only in stands of mesquite near Camp 1, as follows: July 7, two pairs seen, from which a breeding female was taken; July 8, three birds seen. Specimen: ♀, 38933, edematous brood patch, 36.5 gm., Camp 1, July 7. Intergrades between the present subspecies and *R. c. coccinea* of Veracruz are reported from Altamira, Tamaulipas (Mexican Check-list, 1957:329).

Mammals

Dasypus novemcinctus mexicanus Peters: Nine-banded Armadillo.—Remains of an armadillo (89017) were found in a mesquite thicket in the dunes near Camp 1 on July 7. The bones are not badly weathered and were not embedded in sand.

This species has not been recorded previously on the barrier

island of Tamaulipas, nor, for that matter, on any of the barrier islands on the western shore of the Gulf of Mexico.

Lepus californicus merriami Mearns: Black-tailed Jackrabbit.—From two to four individuals were recorded daily in dunes and on alkaline flats in the vicinity of stands of mesquite and cactus.

Specimens (2): ♀ adult, 89018, pregnant (two embryos, 28 mm. in crown-rump length), Camp 1, July 6. Male immature, 89019, Camp 1, July 7. Our specimens have been compared with two skins of *L. c. curti* from the type locality at Eighth Pass, with which they agree reasonably well in color. The size of the adult female is about that characteristic of other specimens of adult *L. c. curti*, but characters of the skull are consistent with those of *L. c. merriami*.

A specimen of this species from Matamoros and several from Brownsville, Texas, have been assigned by Hall (1951:43) to *L. c. merriami*. Specimens from Padre Island, Texas, reportedly resemble *L. c. curti* in smallness of the tympanic bullae but are in other characters referable to *L. c. merriami* (Hall, 1951:44).

Spermophilus spilosoma annectens (Merriam): Spotted Ground Squirrel.—These squirrels were moderately common in dunes at both camps. They were heard calling, and many tracks and holes were seen. On July 7, at Camp 1, a lactating, adult female (89020) and two dependent juveniles (89021, skull only, 89022, skin and skull) were shot at the entrance of a burrow; the uterus of the adult showed six placental scars.

Our adult specimen has been compared with ten specimens obtained by Hall and von Wedel at Eighth Pass in March, 1950; ours differs from the ten in being paler and slightly larger. The pallor is perhaps attributable to seasonal variation, and the size (246-79-38-7; weight, 133 gm.) is within limits that would be expected in a larger series of the population sampled by Hall and von Wedel. Hall (1951:38) referred specimens of this squirrel from Eighth Pass to *S. s. annectens*.

Geomys personatus personatus True: Texas Pocket Gopher.—This pocket gopher was abundant on low, stabilized dunes on the barrier island from four to 73 miles south of Washington Beach. One of us (Wilks) made a trip down the beach on May 20 and 21, 1961, and collected specimens at localities four miles south and 33 miles south of Washington Beach; additional specimens were taken at both Camp 1 and Camp 2 from July 6 to 10. At these localities the gophers seemed to maintain population densities approximating

those of *G. personatus* on Padre and Mustang islands on the Texan coast.

There is but one other record of the Texas Pocket Gopher from México. Goldman (1915) described *G. p. tropicalis* from Altamira on the basis of specimens collected in 1898. Since that time, the species has not been reported as occurring south of Cameron County, Texas (Kennerly, 1954), some 50 miles northwest of the closest station of occurrence of the gophers on the barrier beach of Tamaulipas.

Our specimens are slightly smaller than *G. p. personatus* and slightly larger than *G. p. megapotamus*, the subspecies of nearest geographic occurrence to the barrier island. The degree to which our specimens differ in other respects, such as configuration of the pterygoid, is being studied further by Wilks. For the present, reference of our material to the nominate subspecies best expresses the relationships of these coastal gophers.

The fact that pocket gophers from the Tamaulipan barrier island occupy a position geographically intermediate between present Texan populations and the isolated population in southern Tamaulipas (*G. p. tropicalis*) helps explain the origin of the latter. It is likely that *G. p. tropicalis* represents the southern remnant of a once continuously-distributed population of pocket gophers living in coastal Tamaulipas in mid-Wisconsin to late Wisconsin time. At that time, sea level is thought to have been considerably lower than at present, exposing a sandy strip 80 to 100 miles wide off the present coastline. Presumably this would have been an area suitable for gophers and for southward dispersal of individuals from Texas. The only conceivable barrier to dispersal, and thus to a panmictic population, would have been the Rio Grande, but over the wide, low and sandy coastal plain the river channel almost certainly shifted regularly, thus decreasing its effectiveness as a barrier to movement. With subsequent rise in sea level, the gophers at Altamira became isolated and have presumably remained so for a considerable time. To judge by the marked morphologic differentiation of *G. p. tropicalis*, its degree of isolation from other populations has been much greater than those of populations inhabiting the Tamaulipan barrier island and the barrier islands of the coast of Texas. Contact between the latter two populations was probably fairly regular before man's stabilization of the channel of the lowermost reaches of the Rio Grande.

At Camp 1 we found evidence of the former occurrence of gophers

in an area now largely covered by active beach dunes. Numerous skeletal parts of gophers and "fossilized" burrows (Plate 8) were found on the surface where troughs between active dunes reached down to an older, darker, and more tightly cemented layer of sand underlying the present dunes. It is clear that these gophers were not transported there, because the bones were not damaged, some of the skeletons were almost complete, and many of the bones were found near the "fossilized" burrows. Weathered but well preserved skeletal remains of at least 12 gophers were picked up at this site.

Specimens (17): ♀, 89023, Camp 1, May 20. 4 ♀ ♀, 89024-026, 89029; 3 ♂ ♂, 89027, 89028, 89030; Camp 1, May 21. Male, 89031, Camp 1, July 6. Three ♂ ♂, 89032, 89035, 89038; 4 ♀ ♀, 89033, 89034, 89036, 89037; Camp 2, July 9. Female, 89039, Camp 2, July 10.

Perognathus merriami merriami Allen: Merriam Pocket Mouse. —An individual taken in a trap in the dunes near Camp 2 constitutes the first record of this species from the barrier island of Tamaulipas. This pocket mouse seems to be uncommon on other barrier islands of the western Gulf of Mexico, for there is only one published report of its occurrence on Padre Island, Texas (Bailey, 1905:141). Other nearby stations of occurrence are Altamira, Tamaulipas (Hall and Kelson, 1960:477), Brownsville, Texas (Bailey, *loc. cit.*), and 17 miles northwest of Edinburg, Texas (Blair, 1952:240).

Specimen: sex?, 89040, skull only, Camp 2, July 10.

Dipodomys ordii parvabullatus Hall: Ord Kangaroo Rat.—We found this species uncommon and confined in distribution to dunes, in which it was recorded as follows: an adult female was shot and two other individuals were seen at night on July 6 at Camp 1; three were trapped near Camp 1 on July 7; two were trapped at Camp 2 on July 10.

Specimens (5): ♀, 89041, 2 placental scars, 46 gm., Camp 1, July 6. Male, 89042, testes scrotal, 47 gm.; ♂, 89044, 60 gm.; ♀, 89043, 44 gm.; Camp 1, July 7. Sex?, 89045, skel. only, Camp 2, July 10.

Our material does not differ significantly from specimens obtained by Hall and von Wedel at Boca Jésus María in March, 1950, which formed the basis for Hall's description (1951:41) of *D. o. parvabullatus*. This subspecies is presumably confined in distribution to the barrier island of Tamaulipas. Two immature specimens from Bagdad, Tamaulipas, were tentatively assigned by Hall (1951:41)

to *D. o. compactus,* a subspecies known otherwise only from Padre Island, Texas.

Neotoma micropus micropus Baird: Southern Plains Woodrat.—This species was noted only near Camp 1, where numerous houses were seen in stands of mesquite and prickly-pear cactus and an adult male (89046, 330 gm.) was taken on July 6. This species has not been reported previously from the barrier island of Tamaulipas. Our specimen is referable to the nominate subspecies and shows no approach to *N. m. littoralis,* a subspecies known only from the type locality at Altamira, Tamaulipas (see map, Hall and Kelson, 1960: 684).

Procyon lotor (Linnaeus): Raccoon.—A weathered skull and a broken humerus were found at Camp 2. The skull is being studied by Dr. E. L. Lundelius, who informs us that it matches a number of raccoon skulls found in archaeological sites along the Balcones Escarpment of Texas. Such skulls are larger than skulls of raccoons occurring today in Texas (*P. l. fuscipes*) and closely resemble skulls of raccoons (*P. l. excelsus*) presently confined in distribution to Idaho, eastern Oregon, and eastern Washington. Further details of this situation are to be reported elsewhere by Lundelius.

Taxidea taxus (Schreber): Badger.—Two burrows were found in the stabilized dunes near Camp 1, tracks were noted on the alkaline flats, and a weathered skull (89047) was found on the flats west of Camp 1 on July 7. The skull appears to be of an immature animal, for the sutures are not well closed and the teeth show little wear.

Our records require an extension of known range of this species southeasterly by approximately 50 miles. The only previous record in coastal Tamaulipas is based on two skulls from Matamoros (Schantz, 1949:301). The skull from the barrier island cannot be determined to subspecies but on geographic grounds is referable to *T. t. littoralis,* with type locality at Corpus Christi, Texas.

Canis sp.—Numerous tracks made either by Coyotes (*C. latrans* Say) or by domestic dogs were seen in dunes and on the beach at both camps. A weathered, posterior part of a canid skull was found in dunes at Camp 2 on July 10, and a partial left mandible was taken on the beach at Camp 1 on July 6. Unfortunately, specific identification of the skull fragments is not possible, but the few reasonably good characters that we can use suggest that our material is of domestic dogs rather than of Coyotes. Hall (1951:37) found tracks and other signs of Coyotes at Eighth Pass but did not take specimens.

Most of the canid scats examined by us contained remains of crabs and fishes.

Odocoileus virginianus (Boddaert): White-tailed Deer.—A weathered Recent fragment of a mandible (89048) and part of a femur (89049) of this species were found near Camp 1 on July 7, and a metapodal was picked up in the dunes at Camp 2 on July 9. This species has not been reported previously on the barrier island of Tamaulipas and it probably no longer occurs there, for we saw no tracks or other signs of it. Hall (1951) did not find it at Eighth Pass.

Our specimens probably pertain to *O. v. texanus* but are possibly of *O. v. veraecrucis*, which has been reported from Soto la Marina (Goldman and Kellogg, 1940:89).

The only species of mammal known from the barrier island of Tamaulipas that we did not find is the Hispid Cotton Rat (*Sigmodon hispidus*). Two specimens of this species trapped near Eighth Pass in March, 1950, formed the basis for the description of *S. h. solus* (Hall, 1951:42), a subspecies known only from the type locality.

Discussion

The known vertebrate fauna of the barrier island of Tamaulipas consists of one species of tortoise, two species of lizards, at least one (unidentified) species of snake, 49 species of birds (48 recorded by us and the Semipalmated Sandpiper), and 12 species of mammals. This is clearly a depauperate fauna, such as is characteristic of islands generally, and indicates that the peninsular nature of the northern part of the barrier island is of relatively small consequence in determining presence or absence of species. It is likely that the restricted environmental spectrum is much more important in this regard than is the fact of semi-isolation.

Of the 49 species of birds, 10 are known to breed on the island and an additional 21 are suspected of breeding either on the island or on small islets in the adjacent Laguna Madre de Tamaulipas. Eleven species occur on the island as nonbreeding summer residents, about which we will have more to say below. Four species have been recorded on the island in summer but breed elsewhere, that is to say, they only wander over the island (Man-o'-war Bird, Turkey Vulture, *etc.*). Two species are known only as migrants, and the status of one, the Sora Rail, is uncertain. The number of migrant species doubtless will be greatly increased by field work at those times when birds migrate.

The avifauna is not depauperate owing to the exclusion of any one of the three major zoogeographic stocks thought to be important in the development of the present North American avifauna (Mayr, 1946). If we examine the breeding passerine birds of the barrier island and the breeding passerine assemblage at the same latitude in lowland Sonora (Mayr, *loc. cit.*) as to their ultimate evolutionary sources, we find that for both places somewhat more than half the birds have developed from indigenous, North American stocks, about one-third have been derived from South American stocks, and one-fifth to one-eighth are from Eurasian stocks. It is most unlikely that such close correspondence in relative composition of the two avifaunas would occur by chance. Thus, we can only conclude that each of the historical avian stocks is proportionately restricted in numbers on the barrier island.

Faunistically, the barrier island resembles Padre and Mustang islands and the adjacent mainland of Tamaulipas and southern Texas, reflecting the relative uniformity of environment in this region. It is apparent that there is a faunal "break" or region of transition in the vicinity of Tampico, in extreme southeastern Tamaulipas. On the coastal plain, many tropical species and subspecies occurring in Veracruz are found north to Tampico but fail to extend farther northward to the barrier island of northeastern Tamaulipas. Axtell and Wasserman (1953:4-5), have already commented on this situation, mentioning a number of snakes and lizards that have differentiated subspecifically on opposing sides of the Tampican region. They also note that large numbers of the lowland Neotropical floral and faunal elements reach their northern limits of distribution within the zone of transition around Tampico, and, also, many Nearctic elements find their southern distributional limits there.

Our small samples of birds and reptiles from the island show no detectable morphological differentiation from adjacent populations. However, several of the mammals are moderately-well differentiated, but the patterns and degrees of geographic variation are such that we can only speculate on the historical derivation of the insular populations. *Lepus californicus curti* is presently known only from the barrier island of Tamaulipas, but Hall (1951:43) has suggested that it may also occur on the adjacent mainland. A resemblance between individuals of this subspecies and specimens of *L. c. merriami* from Padre Island in smallness of the tympanic bullae is regarded, probably correctly, by Hall (1951:44) as independent

development—that is, parallel adaptation to similar environmental conditions reaching fullest expression on the barrier island of Tamaulipas. As is also true with *Geomys personatus* and *Neotoma micropus,* the barrier island population of *Lepus californicus* shows relationships with animals from Texas and northern Tamaulipas (*L. c. merriami*) and no connection with (resemblance to) animals from the south (*L. c. altamirae,* known only from the type locality at Altamira, near Tampico).

In color and cranial proportions, *Dipodomys ordii parvabullatus* of the barrier island is closer to *D. o. compactus* of Padre Island than to *D. o. sennetti* of southern Texas and the Tamaulipan mainland. But, *D. o. parvabullatus* resembles *D. o. sennetti* in external measurements (Hall, 1951:39). Possibly *D. o. parvabullatus* and *D. o. compactus* are phylogentically closer to one another than is either to *D. o. sennetti.* It is also possible that each evolved independently from a mainland stock represented today by *D. o. sennetti;* the resemblance of the two insular populations would thus be a matter of convergence in response to like environmental conditions.

Sigmodon hispidus solus is an insular differentiate that probably reached the barrier island from the adjacent mainland of Tamaulipas, where its apparent closest relative, as judged by morphological similarity, now occurs.

Nonbreeding shorebirds in summer south of breeding ranges.—Certain aspects of this subject have already been discussed by Eisenmann (1951). As he notes, the phenomenon is more regular and widespread than generally has been appreciated. The old idea, that such oversummering individuals were "abnormal" or "senile," is totally inadequate, especially in view of the frequently large numbers of individuals involved.

Eisenmann's suggestion that nonbreeders are immature is probably valid, and it is supported by Pitelka's examination of dowitchers (1950:28, 51). For gulls, which can be aged by characters of plumage, there is no question that most nonbreeders are immature. Unfortunately, there are few criteria for determination of age in charadriiform birds.

With the possible exception of a specimen of *Limosa fedoa,* none of the presumed nonbreeding, oversummering shorebirds collected by us showed gonadal enlargement above expected minimal sizes for the species. Even so, the season was late at the time when we were on the island and most of the birds were molting; it is possible their gonads had been enlarged earlier in the season. Behle and

Selander (1953) and Johnston (1956) have shown that nonbreeding first-, second-, and third-year California Gulls (*Larus californicus*) undergo gonadal enlargement in summer. Additionally, nonbreeding first-year males of certain passerine species (for example, the Brown Jay, *Psilorhinus morio;* Selander, 1959) are known to experience partial gonadal recrudescence in summer. It would be useful, and would facilitate discussion, to have data on gonadal condition of oversummering birds; any functional enlargement would be worth documenting.

Some species, notably the Semipalmated Sandpiper, Semipalmated Plover, and Black Tern, oversummer as nonbreeders in such large numbers that it is obvious that a significant fraction of the total population of the species does not breed in any one year. This raises questions concerning the possible ecologic situations that would select for delay in time of recruitment of young birds into the breeding segment of the population, assuming that nonbreeders are immature birds. Delay in maturation, or slow rates of maturation, may show general relationship to paucity of sites of breeding, as Orians (1961:308) suggests, but the shorebirds with which we are dealing breed in regions or in habitat-types not characteristically imposing general restriction on sites of nesting; more than one answer is necessary for the question even at this level. Data on age and numbers of nonbreeders, as well as on the ecology of breeding populations, are critical and are badly needed for most species.

In any event, species for which we have data demonstrating that they regularly oversummer south of their breeding ranges are probably adapted to having a part of their populations refrain from breeding each year. Whether this phenomenon can be explained solely in terms of selection at the level of individual birds (Lack, 1954) or involves selection of an adaptive response of the population as a whole (Wynne-Edwards, 1955; see also Taylor, 1961, concerning *Rattus*) is a problem that cannot be resolved at this time. We may note that the species involved ordinarily breed in arctic and subarctic regions, and it would seem advantageous (as set forth below) for nonbreeders to remain well south of such high latitudes. The numbers of oversummering individuals may fluctuate with over-all population density, possibly as a result of crude density, but possibly also as a result of emigration of individuals in excess of optimal density on breeding grounds (see Wynne-Edwards, 1959). One aspect of this phenomenon not explicitly discussed by Wynne-Edwards is the possibility that some individuals never move north to breeding grounds at all, perhaps as a result of a behavioral char-

acter genetically-grounded and mediated by delayed maturation of the neurohumoral "clock." This certainly would be an economical means by which population numbers could be regulated, for there would be a saving of energy in that some individuals not only would not move north, but also would not participate in the behavioral interactions involved in territorial spacing. Occurrence of these birds throughout southern North America, Middle America, and northern South America may thus reasonably be understood.

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Teeth of Edestid Sharks

BY

THEODORE H. EATON, JR.

The Edestidae are a family of Paleozoic sharks, known from rocks of Mississippian to Late Permian age, and characterized by a series of median, symphysial teeth of specialized structure. In *Edestus* such teeth occur in both the upper and the lower jaw, but in other genera it is not yet certain whether those of the two jaws are alike. Several genera have been described from single sets of symphysial teeth, presumably belonging to the lower jaw. Sets of lateral teeth of the lower jaw are known in *Campodus* (*Agassizodus*), associated with the symphysial series. In this genus the structure and arrangement of the symphysial series are not radically different from those of the lateral teeth, but in other genera the symphysials are increasingly modified until, in the Permian *Helicoprion,* an extraordinary spiral band of teeth is formed in the symphysis, the function and position of which have been difficult to determine.

Moy-Thomas (1939) divided the Chondrichthyes into two orders, presumed to represent divergent evolutionary lines, on the basis of tooth structures. One, the Bradyodonti (proposed on different grounds by Woodward, 1921), comprised sharks in which the outer layer of the tooth was of hard dentine containing vertical tubules, but without enamel. Moy-Thomas included in the Bradyodonti the Edestidae and Orodontidae, as well as the Petalodontidae, Cochliodontidae, Psammodontidae and Copodontidae (following Woodward), and he added also the Holocephali. Radinsky (1961) investigated tooth histology in Chondrichthyes, and concluded that the order Bradyodonti is probably artificial, that it cannot be defined by the character of "tubular dentine," and that it should not include Edestidae and Orodontidae. He suggests that the name Bradyodonti be retained, however, for the four families designated by Woodward, "on the basis of slowness of tooth replacement," and that the Bradyodonti be "included with chimaeroids under the term Holocephali . . . Until further evidence is found, it is suggested that the edestids be kept as a separate group, related to hybodonts and heterodonts."

Accepting this idea, we nevertheless meet other difficulties in attempting to understand the Edestidae. Little material other than teeth has been found, but probably certain fin-spines and denticles known under other names will eventually be associated with Edestid

teeth. Lateral and symphysial teeth are seldom found in association with each other, and this circumstance has resulted in confusion of some generic names, as described on pages 350 and 351. A new species of *Fadenia*, based on symphysial teeth, is named and described farther on. The arrangement of the symphysial teeth in this family has been the subject of prolonged controversy, now diminished as a result of the general agreement of authors that these teeth belong in the median line of the lower jaw, and that the upper jaw also bears a series of symphysial teeth. But the direction in which the series are oriented, and the manner in which the *Helicoprion* spiral evolved from the simpler patterns seen in other genera, have not been demonstrated satisfactorily. A solution to these problems is proposed in the last part of this paper. The illustrations were prepared by Merton C. Bowman.

Obruchev (1953), in a monograph devoted primarily to the work and discoveries of A. P. Karpinsky, reviewed much of the history of investigations of the Edestidae. Without adding conclusions or data of his own, he compiled most of the information so far published, with excerpts from unpublished correspondence of Karpinsky and others, in a useful summary of the subject. As this publication, in Russian, may not be conveniently available to many students in the United States, several figures have been redrawn from it for the present paper. The value of Obruchev's work seems to be as a historical source rather than a contribution of new evidence or interpretations.

Status of Campodus and Agassizodus

DeKoninck (1844:618) described the genus *Campodus* on the basis of scattered teeth (*C. agassizianus*) found in "calcareous nodules in the black shale of Chokier, underneath the coal formation" (translated), in the Lower Westphalian or Namurian beds of Belgium, early Pennsylvanian in age. The teeth are weakly arched, oblong, up to about 15 mm. in length, and surmounted by a small series of hard, shiny tubercles, each of which is also oblong but with its axis transverse to that of the tooth. The tubercles themselves bear minute ridges, and similar ridges are seen also in the depressions between the tubercles. Other, much larger ridged teeth were intermingled with these, but were referred by DeKoninck to *Orodus ramosus* Agassiz.

Teeth apparently congeneric with the latter were described from the Mississippian of Illinois by Newberry and Worthen (1870:358), as *O. corrugatus*. The same authors also described, but with some

hesitation regarding its generic distinctness, a series of teeth from the Pennsylvanian of Illinois under the name *Lophodus variabilis* (1870:360). In 1875, however, St. John and Worthen, finding that the name *Lophodus* was preoccupied, proposed the genus *Agassizodus* for *L. variabilis,* and included in the same genus *O. corrugatus* and two other species. These authors illustrated a large mandible of *A. variabilis* bearing numerous rows of teeth (St. John and Worthen, 1875, pl. 8, fig. 1). The middle row contains the largest teeth, but towards both ends of the mandible the teeth become much reduced and show a form much like those named *Campodus* by DeKoninck; the specimen was found in Upper Pennsylvanian beds near Osage, Kansas.

Lohest (1884) examined DeKoninck's specimens of *Campodus agassizianus,* obtained more material from the beds at Chokier, and was authorized by DeKoninck to continue the description of the genus. His figures show teeth closely comparable to the American *Agassizodus,* and an almost complete intergradation between these and the specimens of DeKoninck's *Campodus.* There can be little doubt that the teeth figured by Lohest all belong to one species, if not to one individual. Lohest concluded that the name *Campodus* should apply both to DeKoninck's *C. agassizianus* and to the American species of *Agassizodus.* After study of the figures published by the authors mentioned, and by Eastman (1902, 1903) and other more recent writers, as well as of the material in the collection of the Museum of Natural History, University of Kansas, I am convinced that Lohest was correct, and shall therefore refer to species that have been described under the name *Agassizodus* as *Campodus.* Most authors subsequent to Lohest (except Eastman) have continued to recognize *Agassizodus,* however. Probably this is because the smallest teeth in the jaws, when present, have not been compared in detail with DeKoninck's series, or have not been illustrated with sufficient care to enable others to notice the resemblance.

Nielsen (1932), in a review of the literature on Edestid teeth, justified the name *Agassizodus* on the ground that symphysial teeth show generic characters better than lateral teeth, and that whereas symphysials were known for the American *Agassizodus,* none were as yet available for *Campodus.* This view disregards Lohest's evidence, which appears satisfactory, that there was no basis for separating the two genera in the first place, inasmuch as the broad range of variation of the lateral teeth in both encompasses the same characters. Neither *Campodus* nor *Agassizodus* was founded upon symphysial teeth.

Symphysial teeth of *Campodus variabilis* have been figured by Eastman (1902, pl. 1, 2, 3; 1903, pl. 1). Isolated symphysial teeth of the same species are in the KU collection (Fig. 1). St. John and Worthen (1875, pl. 8, fig. 24) illustrated an imperfect symphysial tooth of more massive form, with a thicker median knob,

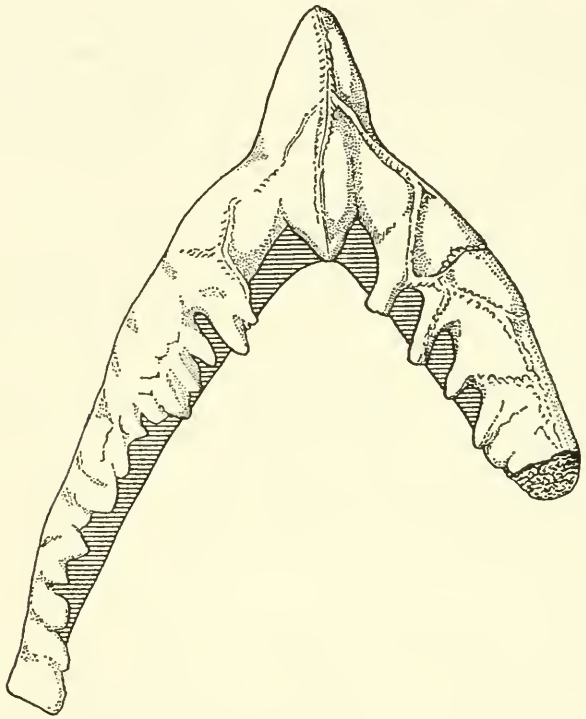

Fig. 1.—*Campodus variabilis,* symphysial tooth, posterior aspect. KU 1056, × 1.5.

as "*A.*" *corrugatus.* Nielsen (1932:37) doubted that this could belong to the same genus as the lateral teeth so named, but I see no reason to question it.

A New Species of Fadenia

Among the Lower Permian fishes described by Nielsen (1932) from East Greenland were two species of Edestidae, both represented by an abundance of teeth. One he named *Agassizodus gronlandicus* (here regarded as *Campodus*), and the other *Fadenia*

crenulata. In the latter the symphysial teeth are much more massive, both in the crown and in the steep lateral flanges, than those of *Campodus.* The median peaks are blunt, the anterior and posterior edges of the flanges of each tooth are crenulated, the anterior most strongly, and the lateral surfaces of the flanges are flattened and bear horizontal wrinkles (Nielsen, 1932, pl. 4, figs. 1, 2, 9-12).

Nielsen's characterization of *Fadenia* is quoted: "Symphysial teeth (at least of one jaw) disposed in an unpaired row, not fused with each other, and of a bilaterally symmetrical shape. Crown of the symphysial teeth as normally in the Edestids developed in such a way that its right and left halves meet in an acute angle forming a pronounced rostro-caudal edge. . . . Crown of the symphysial teeth at the median plane broader than one half of the length, with the labial margin much and the lingual margin only slightly folded, and with a sculpture of plicae, which, possibly on account of wear, are much less distinct on the highest median than on the lowest lateral parts. . . ." He describes and figures both the symphysial and the lateral teeth, but inasmuch as no lateral teeth accompany the specimens to be described here, only the symphysials are pertinent. Nielsen also remarks that there is less difference between the lateral and symphysial teeth of *Fadenia* than between those of any other edestid, and this genus must therefore be the most primitive one known in the family. The type species, *F. crenulata,* was found in Pennsylvanian limestone, Cape Stosch, East Greenland.

Two specimens in the Museum of Natural History, University of Kansas, have characters that place them in *Fadenia* rather than *Campodus,* and are described here as

Fadenia gigas new species

Type: Two symphysial teeth in place on a block of osteodentine (Fig. 2); No. 1023, Museum of Natural History, The University of Kansas; found 4 feet below top of Cherokee shale (Lexington coal), Lower Pennsylvanian, at Lucas, Henry County, Missouri. There is no information as to the collector or date.

Diagnosis: The teeth resemble those of *F. crenulata* in proportions and shape, in having a rostro-caudal edge in the median line, and in a sculpturing of plicae on the lateral surfaces. But they differ in having both the labial and the lingual margins much folded, and in being of far greater size (*gigas,* Greek, giant). The height of the more complete tooth is 79 mm., not including a small part of the tip that is missing; its anteroposterior breadth in the median plane is 45 mm. These measurements contrast with 23 and 15.5 mm., respectively, as determined from Nielsen's fig. 12 on plate 4.

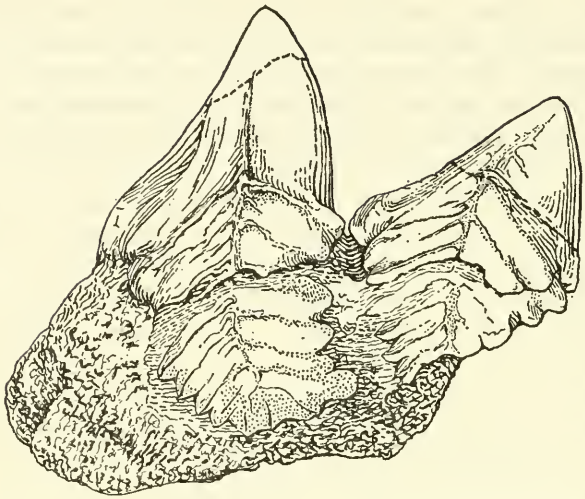

Fig. 2.—*Fadenia gigas,* new species, symphysial teeth, right side. KU 1023, × 0.65.

Referred specimen: KU 865, consisting of two symphysial teeth, attached to a block of osteodentine, that are smaller than those of the type. The folds of the anterior and posterior margins are farther apart and less numerous than in the type, but the general shape and the pattern of plicae on the surface closely resemble it. There is no information on the source of this specimen, but its form, color, and mode of preservation strongly suggest that it came from the same horizon as the type. Probably the specimens pertain to different regions of the symphysial series, but there is no evidence to show whether the series formed a simple arch or a spiral; the former, to judge from Nielsen's *F. crenulata,* is more probable. The shark from which they came must have been large, perhaps four or five meters in length, to accommodate a series of such massive teeth and their counterparts in the opposing jaw.

Position and Evolution of the Symphysial Teeth

Neither the orientation of the *Helicoprion* spiral in the animal that carried it, nor the relationship of this curious device to the symphysial series in other edestid sharks seems to have been stated convincingly. In the more generalized members of the family, *Campodus* and *Fadenia,* it is clear that in the lower jaw, at least, a median row of teeth curved forward and outward, that they represented a growth series, and that the more lateral teeth were also arranged in series that curved up and out over the occlusal surface of the mandible. Whether these also were growth series is not entirely clear, but the manner of their replacement may not have been

the same as in most sharks. The symphysial and lateral teeth in *Campodus* and *Fadenia* are not greatly different in structure. A growth series in a modern shark, *Lamna* (Fig. 3), shows the usual method of growth and replacement, the largest teeth being those that have become functional and that will presently be lost.

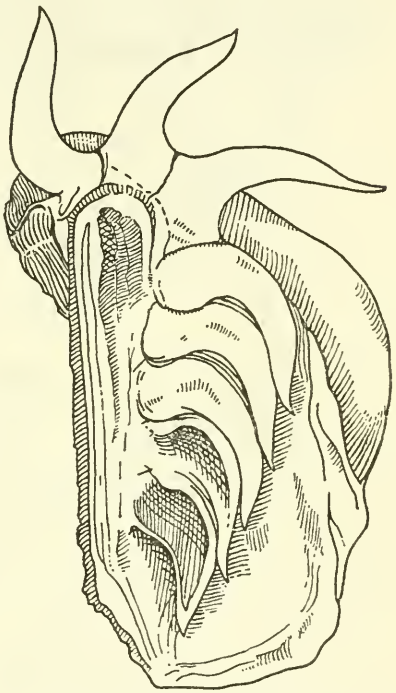

FIG. 3.—Vertical section through developing tooth-series in *Lamna*. Anterior is to left. (After Owen, from Obruchev, 1953.)

In *Edestus mirus* (Fig. 4) Hay (1912) was able to show that both the lower jaw and the upper carried symphysial teeth in long arched series; Hay also made it clear that the upper series was single, like the lower, and not paired (as erroneously stated by Nielsen, 1932:26). The lower ends of the serrated symphysial crowns in *Edestus* turn back, each being overlapped by the tooth behind it, and the osteodentinal bases are partly or completely fused into a curved bar that supports the series. Fig. 5 (Hay, 1909) shows the symphysial series of *E. crenulatus*, and Fig. 6 (Woodward, 1917) shows that of *E. newtoni*. These figures demonstrate the varying curvature of the arch in *Edestus; E. newtoni* seems most nearly to approach the spiral form.

Having established that the lower ends of the crowns, on each side of the bar, turn posteriorly beneath the following teeth, it seems that in the more extended series in *Helicoprion* (Fig. 7) the same characteristic could be used, in the absence of any associated parts of the head, to decide which way is posterior in the functional (largest) teeth of the series, provided that any close relationship exists between these two genera. Hay (1912) decided that this procedure was not acceptable because it led "to the absurd conclusion that the very small teeth of the innermost coil are the

ones that were last formed," and some other, more recent, writers have agreed. If, however, the teeth belong in the mouth and are homologous with those of *Edestus* and other sharks (which cannot be doubted), there are only two possible ways to place them in the symphysis. Either the large teeth are posterior to the sym-

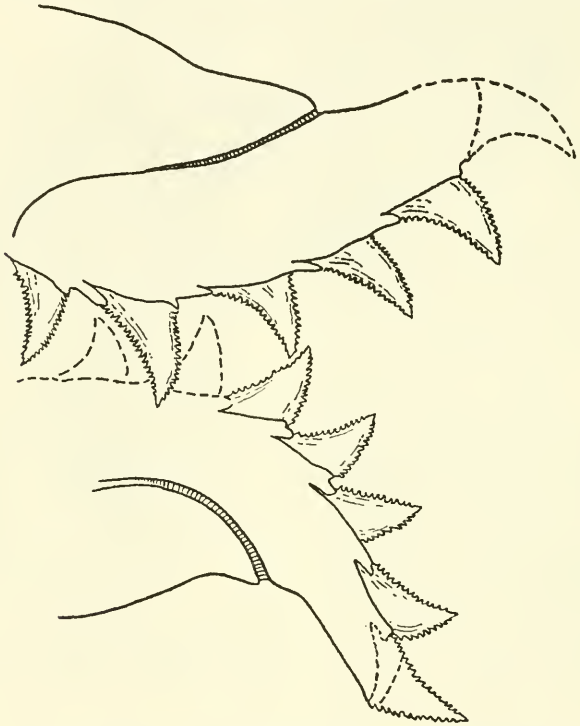

FIG. 4.—*Edestus mirus*, upper and lower symphysial teeth, right side. (After Hay, 1912.) × 0.75.

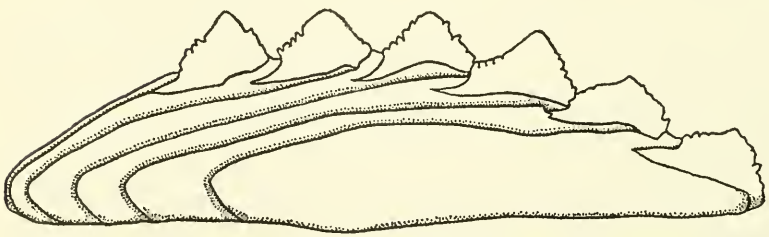

FIG. 5.—*Edestus crenulatus*, symphysial teeth, right side. (After Hay, 1909.) × 0.65.

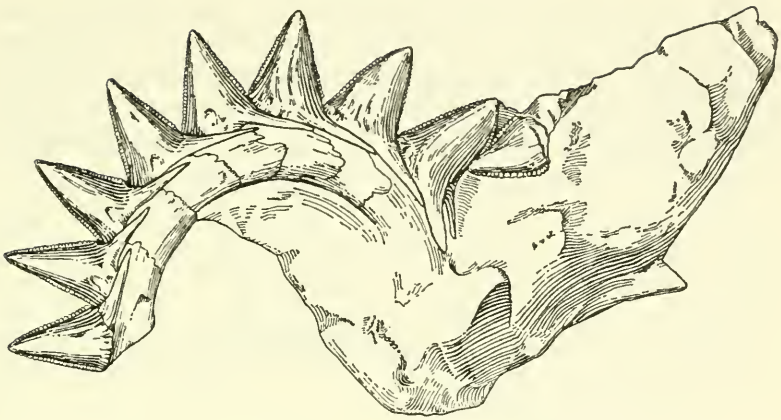

FIG. 6.—*Edestus newtoni,* symphysial teeth, left side. (After Woodward, 1917.) × 0.4.

physis, and the size decreases forward, as teeth that were formerly in use are pushed down, under and inward (the smallest teeth being oldest of all), or the large teeth are anterior, and are followed from behind by a long coiled series of replacing teeth which are still in the earlier stages of growth; in this case the smallest teeth are, indeed, those most recently formed, as is true in all known replacement series in sharks. The teeth come up and forward over the surface of the jaw from behind, and as the older, larger teeth are broken off anteriorly, those behind take their place. This concept is fully in agreement with our information on the teeth of *Edestus,* it accounts for the existence of the spiral as a growth series, and it places *Helicoprion* at the peak of specialization in the family. There is, however, some difficulty in understanding how an arched replacement series evolved into a spiral, and how it is that the youngest tooth-buds come to lie inside of two or more whorls of older teeth.

The key to both problems may lie in the fusion of the bases of the symphysial teeth into a continuous curved rod. The crowns fit against one another, even in early stages of growth, and the rod, at first small, slender, and merely arched, becomes extended as the teeth grow. A given number of teeth occupying a certain distance on the rod at an earlier stage would necessarily occupy a greater space as they grew. Pressure is therefore exerted to make the spiral grow in length, a pressure corresponding to that which

causes the movement of tooth-buds upward in the growth series of such a shark as *Lamna*. In *Helicoprion*, however, the rigidity of the growing spiral rod, formed by fusion of the basal dentine of the teeth, probably compelled an actual movement in two directions during the ontogeny of the shark (Fig. 8). Presuming

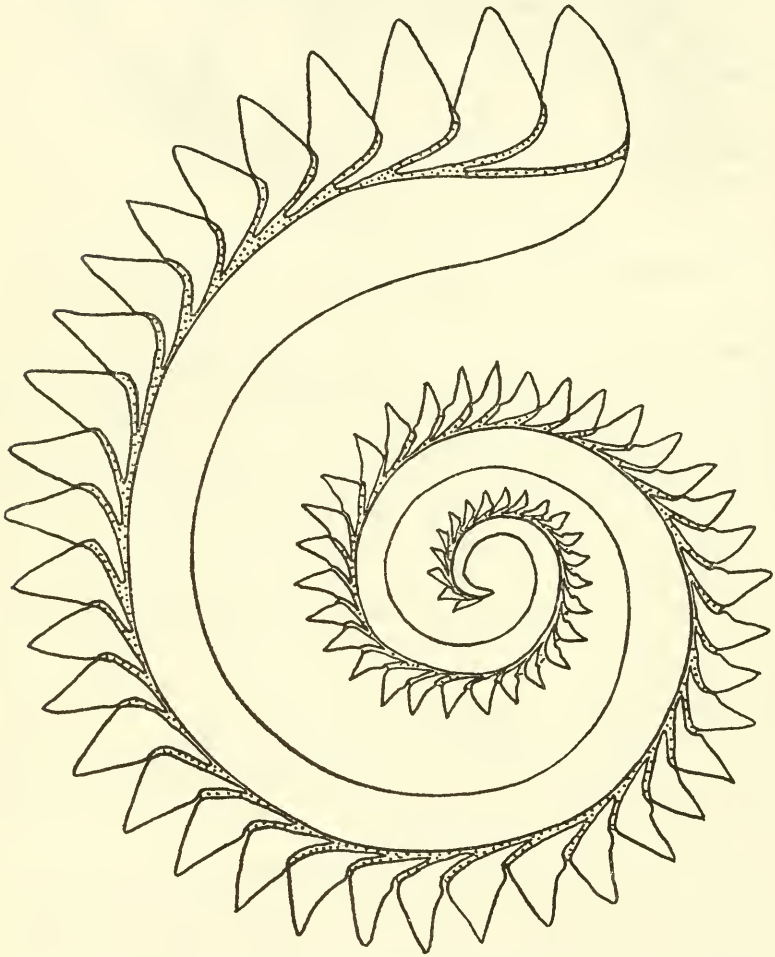

FIG. 7.—*Helicoprion ferrieri*, symphysial teeth, right side. (After Hay, 1909.) Approximately × 1.

that the first stage of formation of the symphysial tooth-row took place on the lingual, or posterior, aspect of the symphysis, as is most probable, and that the rate of growth is greatest in the

youngest individuals, the tendency of the uppermost teeth in the series to move up and forward would be equalled or exceeded by the tendency of the lower part of the series to be pressed down. Since the curvature of the symphysial surface in the youngest individuals is much greater than in older, and since the spiral rod is present upon this surface at an early age, any downward movement compels the series of younger tooth-buds to retreat inward and forward beneath the symphysis, curling eventually up and back, below the functioning row of larger teeth that stand on the occlusal surface. It appears more likely that a row of embryonic tooth-buds would retreat into the tissues of the jaw, forming in a sense a spiral pocket for their development, than that old, used

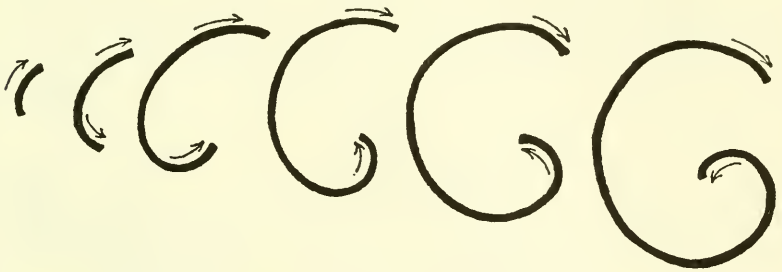

FIG. 8.—*Helicoprion.* Diagram of growth of spiral band of symphysial teeth.

teeth would be forced down into the flesh in a spiral from the anterior end of the functioning tooth-row. If growth, loss and replacement in the symphysial series were rapid, the largest teeth, here considered to have been those at the anterior margin of the jaw, would be replaced frequently as they broke off and the large end of the spiral moved outward.

Evidently in the family Edestidae the food was something that required crushing; there is little difference in the lateral teeth between one genus and another, so far as known. But evolutionary advance in the family was associated with the increasing specialization of the median tooth-series, probably in both upper and lower jaws. This implies that the feeding action involved a different use of the symphysial teeth from that of the lateral series, and in *Edestus* the form suggests a scissorlike motion of the powerful symphysial series in a vertical plane. Presumably the teeth could then be used to cut off or pull away objects growing on a surface (such as mussels, corals, hydroid clusters, stalked barnacles, and

crinoids), or, alternatively, to dig and pull out burrowing clams from mud or sand. It seems more likely that the first of these is correct, and moreover that the teeth did not have a defensive or predatory function.

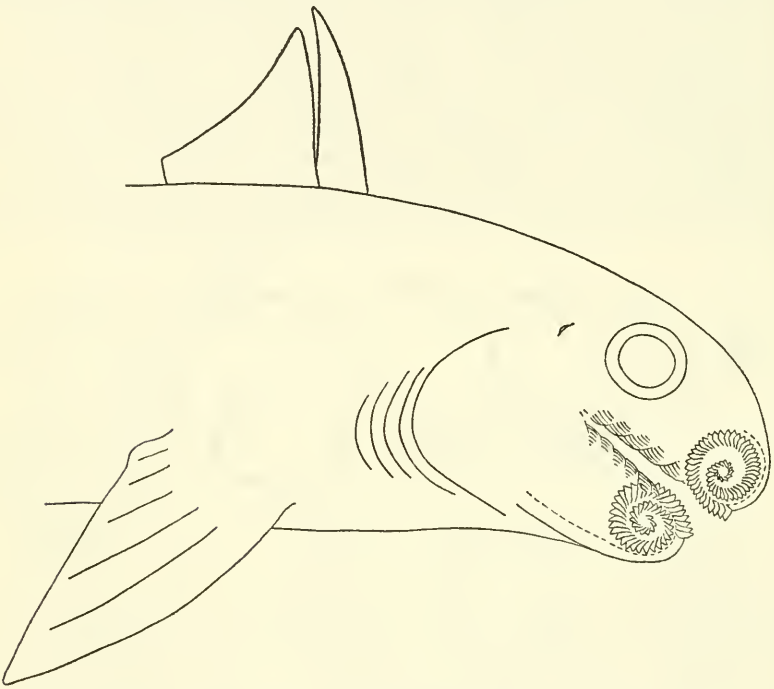

Fig. 9.—Hypothetical reconstruction of *Helicoprion*, showing symphysial teeth.

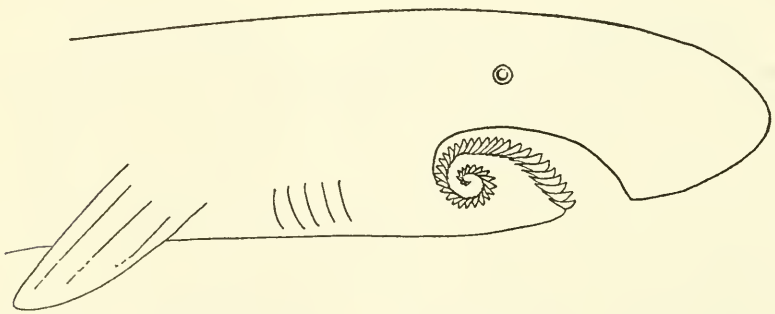

Fig. 10.—Van Den Berg's reconstruction of *Helicoprion*. (From Obruchev, 1953.)

If *Helicoprion* is the end-form of the family in a morphological sense, and if it resembled *Edestus* in having a symphysial series in the upper as well as the lower jaw, then the diagrammatic restoration in Fig. 9 suggests the possible arrangement of the teeth, the head being viewed as a transparent object. Although direct evidence is lacking, there can be little doubt that in support of a mechanism primarily for crushing shells the upper jaw must have been fused with the cranium, as in Holocephali. The only previous figure known to the writer, in which the spiral is shown with the larger teeth forward, is a sketch sent by Van Den Berg to Karpinsky in a letter dated November 21, 1899, reproduced by Obruchev, 1953, and here shown as Fig. 10. In this drawing, however, Van Den Berg appears to have regarded the tooth series as resting upon a median lower jaw, and he did not know that there were also lateral teeth. He compared the spiral to the radula of a gastropod mollusk.

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Variation in the Muscles and Nerves of the Leg in Two Genera of Grouse (Tympanuchus and Pedioecetes)

BY

E. BRUCE HOLMES

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INTRODUCTION

The purposes of this study were: (1) to obtain information on individual variation in the anatomy of the muscles and nerves of the leg of *Tympanuchus cupido pinnatus* (Greater Prairie Chicken), *T. c. attwateri* (Attwater's Prairie Chicken), *T. pallidicinctus* (Lesser Prairie Chicken), and *Pedioecetes phasianellus jamesi* (Sharp-tailed Grouse); (2) to determine whether or not the two species of the genus *Tympanuchus* differ constantly in the myology of the leg; and (3) to determine what constant differences in the myology of the leg exist between the two closely related genera *Tympanuchus* and *Pedioecetes*.

These particular birds were chosen because they are closely related, and closely resemble one another in habitats occupied and in patterns of behavior. It was desired to study examples that showed as few adaptive differences as possible among the grouse. Series of each of the three species of grouse were readily obtainable, making it possible to draw comparisons at the level of individuals, subspecies, species, and genera.

The study here reported on was begun in the spring of 1957 and was completed in the autumn of 1961.

Prior work on the muscles of the leg of birds has been reviewed by Hudson (1937) and Hudson, *et al.* (1959). Only papers dealing with the innervation of the leg in birds are reviewed below.

DeMan (1873) treated the nerves of *Paradisea papuana, Corvus monedula,* and the chicken; he also commented briefly on a few other species. Jhering (Ihering, 1873) briefly described the lumbosacral plexus in approximately a dozen birds, but illustrated only two. Gadow (1880) described the nerves in *Struthio, Rhea,* and *Casuarius;* his paper contains some excellent illustrations of nerves. Unfortunately, the text is marred by numerous confusing typographical errors. Carlsson (1884) described the nerves of *Eudyptes chrysolopha, Alca torda, Mergulus alle,* and *Mormon arcticus.* Gadow (1891) described the nerves in a study that included a large variety of birds, but published few illustrations. DuToit (1913) described the lumbosacral plexus of the chicken. Romer (1927) gave the innervation of the hip and thigh muscles in the chicken, but did not cover the lumbosacral plexus. Appleton (1928) gave the innervation, in various birds, only of those muscles of the hip and thigh that are supplied by the tibial and peroneal nerves; he did not include the lumbosacral plexus. Sudilovskaya (1931) described the nerves of *Struthio, Rhea,* and *Dromaeus* (*Dromiceius*). Unfortunately, his illustrations are almost useless as far as the nerves are concerned. Boas (1933) described the lumbosacral plexus in a large number of birds. His extensive account includes numerous good illustrations. Howell (1938) listed the innervation of the hip and thigh muscles in the chicken; he did not include the lumbosacral plexus. Fisher (1946) listed the innervation of the muscles of vultures, but did not include the lumbosacral plexus. Wilcox (1948) gave the innervation of the muscles

of *Gavia immer*, but did not include the lumbosacral plexus. Fisher and Goodman (1955) described the nerves in the Whooping Crane. Papers by Chomiak (1950) and Yasuda, *et al.* (1959), both dealing with the chicken, were not examined.

MATERIALS AND METHODS

Complete dissections of the muscles and nerves were made in eight legs (of five specimens) of the Lesser Prairie Chicken (*Tympanuchus pallidicinctus*), six legs (of four specimens) of the Greater Prairie Chicken (*T. cupido pinnatus*), three legs (of two specimens) of Attwater's Prairie Chicken (*T. cupido attwateri*), and six legs (of four specimens) of the Sharp-tailed Grouse (*Pedioecetes phasianellus jamesi*).

For convenience and simplicity of reference, each specimen has been designated by a symbol consisting of the first letter of the genus and of the species (and also of the subspecies in *T. cupido*) plus a number. The letter "L" or "R" is added to indicate the left or right leg. Thus the symbol T.p. 1L refers to the left leg of specimen number one of *T. pallidicinctus*.

All specimens are in the University of Kansas Museum of Natural History. The catalogue number of each specimen, and the legs of it that were dissected, are listed below.

T.p. 1L,R	KU38520	T.c.p. 4L	KU38518
T.p. 2L,R	KU38521	T.c.a. 1L,R	KU36617
T.p. 3L,R	KU38522	T.c.a. 2L	KU36618
T.p. 4L	KU38523	P.p. 1L,R	KU38526
T.p. 5R	KU38524	P.p. 2L	KU38527
T.c.p. 1L,R	KU38515	P.p. 3L,R	KU38528
T.c.p. 2L,R	KU38516	P.p. 4L	KU38529
T.c.p. 3L	KU38517		

The specimens were injected in the field either with formalin (10%) or embalming fluid, except for those of *T. c. attwateri*, which were frozen; the latter were later injected with embalming fluid. Injection in all the birds was by hypodermic syringe into all major muscle masses, into the body cavities, and subcutaneously in the neck, wings, and feet. In those specimens injected with embalming fluid, the body cavities were injected with formalin. The embalming fluid consisted of 70 per cent alcohol, glycerin (or propylene glycol), and formalin (full strength) in the approximate ratio of 78:20:2, respectively. This fluid gave good preservation; these specimens had the advantages of lacking almost entirely the irritating odor of formalin and of having pliable tissues. The skin of those specimens originally injected with formalin was slit in several places and they were transferred to crocks containing embalming fluid (without the formalin). After a period of many weeks, with two changes of fluid, most of the formalin odor was eliminated and the muscles were sufficiently pliable to be easily dissected. All specimens were kept in containers filled with embalming fluid. No mold ever appeared, even though no phenol or other chemical was added.

To facilitate comparison, two or three specimens were frequently dissected simultaneously. The nerves and smaller muscles were dissected with the aid of a stereoscopic microscope mounted on a long movable arm. In order satisfactorily to expose the lumbosacral plexus the posterior half of the sternum and pectoral muscles, as well as the abdominal viscera, were removed.

To insure more nearly accurate proportions, drawings of the pelvis and of some of the muscles were made with the aid of photographs of the several specimens listed above.

TERMINOLOGY

Skeleton

The majority of the osteological terms used in the present paper are those used by Howard (1929); however, many skeletal features are not named by Howard. Since names for most of these parts were not found in the other literature examined, it was necessary for me to propose terms for them. Most of this new terminology pertains to the pelvis. All of the osteological terms used in the present paper, whether used by Howard or not, are briefly defined below. Those of the pelvis are illustrated in fig. 1. Most of the remaining terms are illustrated by Howard (1929).

PELVIS

The *median dorsal ridge* is the blunt ridge in the midline of the anterior part of the synsacrum formed by the neural spines of the vertebrae. The *antitrochanter*, on the posterodorsal rim of the acetabulum, is a pyramid-shaped projection that articulates with the proximal end of the femur. The *anterior iliac crest* is a ridge along the dorsomedial border of the ilium, beginning almost at the anterior end of that bone; the crest curves laterally as it extends posteriorly and (for purposes of the present definition) ends at the level of the posterior edge of the antitrochanter, where the crest is continuous with the lateral iliac process. The *lateral iliac process* is a pronounced, laterally or ventrolaterally, projecting ridge on the ventrolateral surface of the ilium posterior to the level of the antitrochanter; the process does not extend as far as the posterior end of the ilium. The *lateral ischiatic ridge* is a relatively slight ridge continuous with the posterior end of the lateral iliac process and curves posteroventrally across the lateral surface of the posterior part of the ischium; the ridge extends to the ventral edge of the ischium in some individuals and not in others. The *dorsolateral iliac ridge* begins at the lateral edge of the ilium near the posterior end of the lateral iliac process and curves posteromedially and somewhat dorsally, extending to the posterior edge of the ilium. The *lateral iliac fossa* is the concavity below the overhanging lateral iliac process. The *ilio-ischiatic fenestra* is a large oblong opening behind the acetabulum between the ilium and the ischium. The *obturator foramen* is a small oval opening posteroventral to the acetabulum between the ischium and the pubis. The *ventral ischiatic tubercle* is the angle formed by the ventrally projecting ischium at the point (near its midlength) where the ischium overlaps and lies lateral to (and fused to) the pubis. The *pectineal process* is an anterolaterally directed projection of the ventrolateral edge of the ilium anteroventral to the acetabulum. The *femoral notch* of the ilium is a shallow notch in the ventrolateral edge of the ilium approximately halfway between the last rib and the pectineal process. The *oblique iliac crest* is a pronounced blunt ridge on the ventral surface of the ilium and extends from the posterolateral corner of the last synsacro-thoraco-lumbar vertebra to near the anteroventral border of the ilio-ischiatic fenestra. The *internal ilio-ischiatic crest* is more or less continuous with the oblique iliac crest and extends posteriorly along the dorsal border of the ischium (forming the ventral border of the ilio-ischiatic fenestra), and then curves sharply dorsomedially onto the ventral surface of the ilium. The *iliac recess* is a concavity dorsolateral to the sharply curving posterior end of the internal ilio-ischiatic crest.

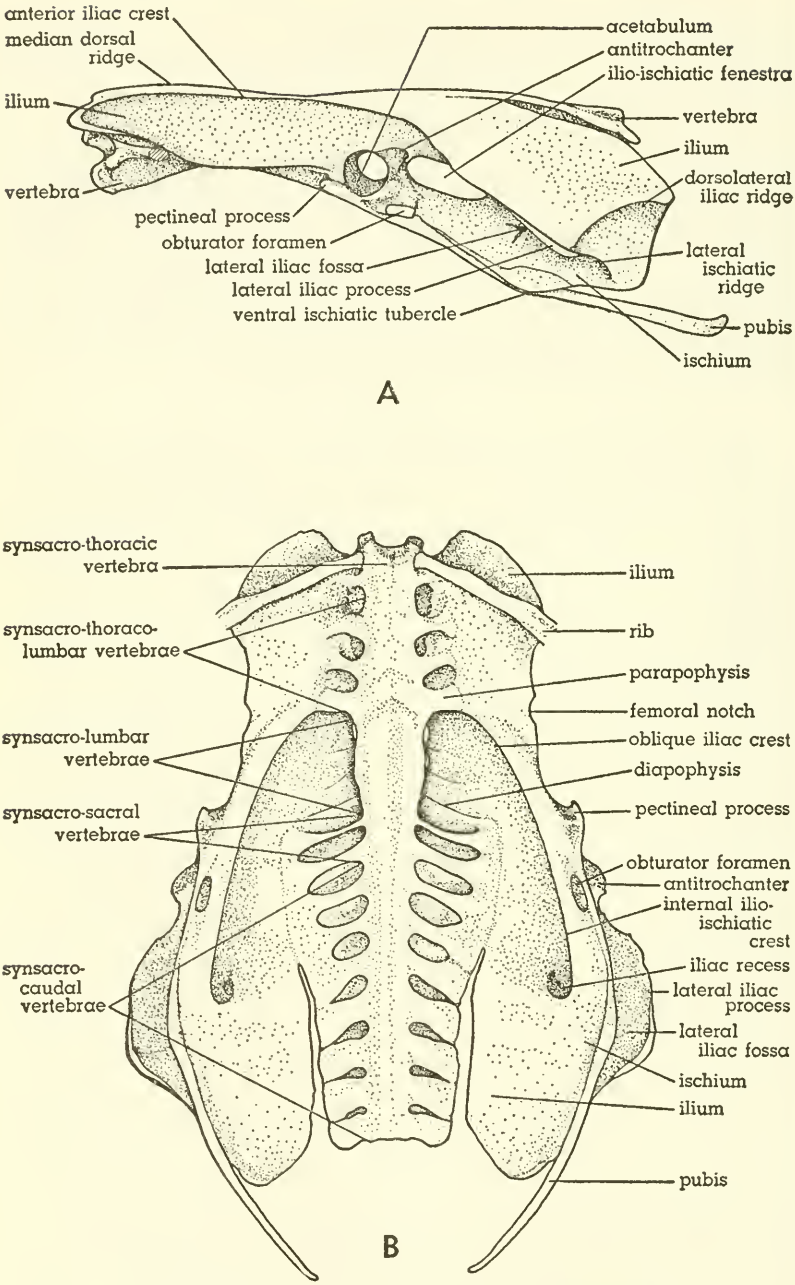

FIG. 1. Pelvis of *Tympanuchus pallidicinctus*. A. Lateral view. × 1. B. Ventral view. × 1⅛.

The terminology applied to the synsacral vertebrae by different authors varies. The terminology proposed by DuToit (1913) is employed in the present account. See my fig. 1B. This terminology differs considerably from that used by Howard (1929). DuToit divides the fused synsacral vertebrae into the following five groups, listed in anteroposterior sequence: (1) *synsacro-thoracic,* which bear movable ribs; (2) *synsacro-thoraco-lumbar,* which lack movable ribs but possess well developed laterally directed parapophyses, in addition to the more dorsally directed diapophyses; (3) *synsacro-lumbar,* which lack parapophyses, although possessing inconspicuous diapophyses; these vertebrae are shortened anteroposteriorly and are so firmly fused together that often the number present can be determined only by counting the intervertebral foramina; (4) *synsacro-sacral,* which have much more pronounced transverse processes than do the synsacro-lumbar vertebrae; these transverse processes are expanded distally where they fuse with the ilium and represent both parapophyses and diapophyses partly or completely fused together plus sacral ribs (detectable only in the embryo); there are considered to be two of these vertebrae; they are situated at approximately the level of the acetabulum; (5) *synsacro-caudal,* which include the remainder of the fused vertebrae; no marked gross morphological features differentiate the synsacro-sacral and the synsacro-caudal groups of vertebrae. The boundaries between all but the last two groups of vertebrae are usually, but not always, easily determined. It may be difficult to determine whether a vertebra with rudimentary parapophyses belongs to the synsacro-thoraco-lumbar or the synsacro-lumbar group. Sometimes a parapophysis will be better developed on one side of a vertebra than on the other.

FEMUR

The *trochanter* is a large squarish tuberosity on the lateral surface of the proximal end of the femur. The *trochanteric ridge* is a sharp, longitudinal (relative to the femur) ridge forming the anterior edge of the trochanter. The *obturator ridge* is a short, blunt, longitudinal ridge forming the posterior edge of the trochanter. The *anterior intermuscular line* is a slight ridge extending distally from the trochanteric ridge. The *posterolateral intermuscular line* is a slight ridge extending distally from the obturator ridge. The *posterior intermuscular line* is a slight, longitudinal ridge on the mid-posterior surface of the femur. The *internal condyle* is a large rounded articular prominence on the medial side of the distal end of the femur. On the lateral side of the distal end of the femur are two articular prominences—the lateralmost, smaller one is the *fibular condyle,* separated by the *fibular groove* (visible from posterior aspect only) from the larger and more medial *external condyle.* The *popliteal area* is a depression on the posterior surface of the distal part of the femur immediately proximal to the condyles.

TIBIOTARSUS AND FIBULA

The *inner cnemial crest* is pronounced and directed anteriorly on the anterior surface of the proximal end of the tibiotarsus. The *outer cnemial crest* is pronounced and directed anterolaterally on the anterolateral surface of the proximal end of the tibiotarsus. The *rotular crest* is transverse and forms the anterior border of the proximal end of the tibiotarsus; the crest extends between the dorsal ends of the two cnemial crests and also extends medial

to the inner cnemial crest. The *fibular crest* is longitudinal on the lateral surface of the tibiotarsus and fuses with the middle part of the fibula. The *fibular tubercle* is small and on the lateral surface of the fibula near the level of the middle of the fibular crest. The *anteromedial intermuscular line* is a slight ridge extending from the inner cnemial crest down the anteromedial surface of the tibiotarsus. The *anterolateral intermuscular line* is a slight ridge extending from the fibular crest down the anterolateral surface of the tibiotarsus. The *supratendinal bridge* is a transverse bony arch over a longitudinal groove near the distal end of the anterior surface of the tibiotarsus.

TARSOMETATARSUS

The *hypotarsus* is a large, pronounced, squarish protuberance on the posterior surface of the proximal end of the tarsometatarsus and contains grooves and canals for the passage of the flexor tendons. The longitudinal ridges forming the lateral and medial edges of the posterior surface of the hypotarsus are termed *calcaneal ridges*. The *posterior metatarsal crest* is long and sharp; it is continuous with the medial calcaneal ridge that extends most of the way down the posterior surface of the tarsometatarsus medial to the midline; there is an opening between this crest and the tarsometatarsus immediately distal to the hypotarsus. The *medial metatarsal depression* is large; it is on the medial surface of the proximal end of the tarsometatarsus. The *anterior metatarsal groove* is a longitudinal groove in the midline of the proximal part of the anterior surface of the tarsometatarsus. The three *trochleae* are large rounded articular prominences at the distal end of the tarsometatarsus; there is one at the base of each of the digits II, III, and IV. The term *distal foramen* (as used by Howard) refers to a short, anteroposteriorly directed canal that perforates the tarsometarsus a short distance proximal to the intertrochlear notch between the trochleae for digits III and IV. Beginning at the middle of this canal and extending distally at a right angle to it is the *intertrochlear canal,* which opens via the terminal foramen into the intertrochlear notch between the trochleae for digits III and IV.

Nerves

For ease of description I have coined terms for the major divisions of the femoral and sciatic nerves.

Muscles

My terminology follows that of Fisher (1946) and Fisher and Goodman (1955) except for Mm. femoritibialis externus, flexor cruris lateralis (accessory head), and obturator internus et externus. Fisher (1946:547) states that most of his names for the hip and thigh muscles are those of Howell (1938) and the names for the shank and foot muscles are those of Hudson (1937). Fisher deviates, without explanation, from Howell's terminology in respect to Mm. vastus medialis and femoritibialis internus, M. caudofemoralis, M. flexor cruris lateralis, and Mm. obturator internus and obturator externus. Fisher's synonymy of these muscles (1946:

table 42) is in error. Fisher understandably deviates from Hudson in respect to Mm. extensor brevis digiti III and extensor proprius digiti III (see Holmes, 1962), although Fisher's synonymy is in error here. See my table 1.

I am not using Fisher and Goodman's term femoritibialis externus; this muscle is here considered as a part of M. vastus lateralis. A great deal of confusion surrounds the terminology of the muscle complex here termed Mm. vastus lateralis and vastus medialis. Hudson (1937), Hudson, *et al.* (1959), Fisher (1946), and Fisher and Goodman (1955) have used different terminology for this complex. Most of the confusion stems from Gadow's (1891) unclear description of this complex, which he subdivided into two units termed Mm. femori-tibialis externus and femori-tibialis medius. Many birds have three parts to this complex. It is difficult to determine how to apply Gadow's two terms to these three parts. As nearly as I can determine, the correct method is that of Hudson, *et al.* (1959); but because Gadow's terms have been used in different ways (even by the same worker), it seems best to abandon these terms. Berger (1956:272) believes that the muscle unit that Fisher and Goodman term M. femoritibialis externus represents a head of M. vastus lateralis; I am accepting his opinion. For the three parts of the complex under discussion, I am using the terms M. vastus medialis and M. vastus lateralis pars lateralis and pars postica.

Fisher (Fisher, 1946; Fisher and Goodman, 1955) considers the muscle here termed M. femorocruralis as an accessory head of M. flexor cruris lateralis. The two muscle units in question are closely associated; they insert broadly on opposite sides of a common tendinous raphe. Howell (1938:73) considers this to be a secondary fusion of unrelated muscles. Romer (1927:366) states that in the chick embryo M. femorocruralis is in reality a shank muscle that migrates into the thigh during development. Therefore, Fisher's usage of a single name for these two unrelated muscles is unsatisfactory. I am using Howell's terminology in which the name flexor cruris lateralis represents the main head only of Fisher's M. flexor cruris lateralis and the name femorocruralis represents Fisher's accessory head.

Gadow (1891) divides the obturator complex into two muscles (or muscle groups), which he terms M. obturator and Mm. accessorii M. obturatoris. He states that the former is homologous with the mammalian obturator internus and the latter with the obturator externus. Hudson (1937), accepting Gadow's homologies, renamed these muscles M. obturator internus and M. obturator externus. Nearly all subsequent workers have followed Hudson's terminology, with its implication that these muscles are homologous with the mammalian muscles of the same name. Howell (1938) is an exception. He points out (pp. 78, 79) that the obturator internus of Hudson is homologous with the obturator externus of mammals. His evidence is convincing: "In origin the obturator is somewhat suggestive of the mammalian obturator internus, for which it has uniformly been mistaken. That the latter interpretation is incorrect, however, is attested by the facts that it receives twigs of n. obturatorius within the pelvis, passes *through* the obturator foramen rather than dorsal to the border of the ischium, and it is segregated from any muscle with tibial innervation. Insertion has shifted only to a slight and unimportant degree as compared with that of the

mammalian obturator externus, and beyond question it is the equivalent of that muscle. The stimulus for a longer muscle, has been the same, resulting in the extension of origin to within the pelvis of the externus in birds and the internus in mammals, but the obturator internus is an extension of a part of the gemellus mass and this does not occur in any vertebrate class but Mammalia." Howell applies the term M. obturator to the entire obturator complex.

Romer (1927), studying the development of the thigh musculature in chick embryos, concluded that the entire obturator complex is homologous with the mammalian obturator externus plus quadratus femoris. He considered the avian M. flexor ischiofemoralis to be the homologue of the mammalian obturator internus.

Gadow, in his work on the ratites (1880:34), states that M. obturator (obturator internus of Hudson) cannot be homologous to the mammalian obturator internus, but must represent the obturator externus. His reasoning is as follows: "Als M. pectineus kann man diesen Muskel nicht auffassen, da er auf der Aussenfläche des Trochanter major inserirt, ferner auch nicht als M. obturator internus der menschlichen Anatomie, da er nicht vom Plexus ischiadicus, sondern vom Plexus cruralis aus innervirt wird. Seiner Innervation und Insertion nach wäre er nur mit dem M. obturator externus zu vergleichen, wobei er seinen Ursprung im Verhältniss zum Menschen nur bedeutend weiter auf das Os ischii und Os pubis distalwärts ausgedehnt hätte und so allerdings der Lage nach mit Ausnahme seines Insertionsdrittels ein 'internus' geworden wäre."

Since Gadow gives different homologues for M. obturator in two of his works (1880 and 1891), one would suspect that he had changed his opinion in the interim; however, there is no evidence that he did so. In 1880 he gives supporting evidence (quoted above) for his view; in 1891 he does not. After describing (1891:173) how the origin of M. obturator in bird ancestors presumably migrated from a location outside the pelvis to a position inside the pelvis prior to the meeting of the pubis and ischium external to the muscle, he states: "Eine ähnliche Entwicklung ist für den *Obturator internus* der Säugethiere anzunehmen, welchem der *M. obturator* der Vögel entspricht." A similar development in mammals is impossible, owing to the different relationship of the muscle to the pelvic bones in this class. Gadow says nothing more about the mammalian homologue of M. obturator. In view of this discrepancy, Gadow can hardly be considered as a supporter of the idea that the avian M. obturator is homologous with the mammalian obturator internus.

The evidence is conclusive, it seems to me, that the obturator internus of Hudson is not homologous with the mammalian obturator internus. Therefore, the term obturator internus is inappropriate for the avian muscle and must be abandoned. I shall follow Howell (1938) in naming the entire obturator complex M. obturator. This term, of course, is not used in the sense in which it is used by Gadow. The use of the term obturator externus for the entire complex is avoided because it may not correspond exactly to the mammalian obturator externus. As mentioned previously, Romer considers the avian muscle to be homologous not only with the mammalian obturator externus but also with the quadratus femoris.

I am following the policy of Wilcox (1948) and Berger (1952) in latinizing the term anterior, changing it to anticus. When preceded by the feminine word pars, the feminine ending is used (antica).

In table 1 my terminology is compared with that of Fisher and Goodman (1955), Howell (1938), Hudson (1937), and Gadow (1891). The terminology of Fisher (1946) is identical with that of Fisher and Goodman (1955) except that in his earlier work Fisher did not describe or name M. femoritibialis externus, and M. lumbricales of his earlier work is not mentioned in his later work. The terminology of Hudson, *et al.* (1959) is identical with that of Hudson (1937) except that the manner in which the femoritibialis complex is subdivided is identical with that of Gadow (1891) and different from that in Hudson's earlier work; also the abbreviations p. ext. and p. int. are substituted in his later paper for pars anterior and pars posterior, respectively, of M. adductor longus et brevis.

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All of the original drawings except fig. 1 were made by me, although the final inking of figs. 12 through 19 was done by Bret Waller. Fig. 1 was drawn by Kay Swearingen.

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SKELETON

Although no special study was made of the skeleton, certain conspicuous variations are discussed here.

There are a few pronounced differences between the pelvis of *Tympanuchus* and that of *Pedioecetes*. Whereas in the former the thick lateral iliac process has a pronounced overhang with the ventral edge lateral to the ischium (fig. 1), in *Pedioecetes* there is no overhang at all and the edge of this process is much thinner. The ischium in *Pedioecetes* is wider (in dorsoventral extent), especially posteriorly, than in *Tympanuchus*. In *Tympanuchus* the posteroventral margin of the ischium is rounded and is free from the pubis, whereas in *Pedioecetes* it is pointed and fused with the pubis.

In *Tympanuchus cupido* (both subspecies) the lateral iliac process extends farther ventrally than in *T. pallidicinctus*, approaching or extending ventral to the level of the pubis in the former species; also the edge of this process is thicker in *T. cupido*.

All specimens studied have a single synsacro-thoracic vertebra. The number of combined synsacro-thoraco-lumbar and synsacro-lumbar vertebrae is eight in each specimen of *Tympanuchus* and in one specimen of *Pedioecetes phasianellus jamesi* and is seven in three specimens of the latter. In most specimens of *Tympanuchus* there are three synsacro-thoraco-lumbar and five synsacro-lumbar vertebrae, although in two specimens (*T. pallidicinctus*) there are four of each group; in one of these latter two specimens the parapophysis on one side of the fourth synsacro-thoraco-lumbar vertebra is small. The first (of five) synsacro-lumbar vertebra has a rudimentary parapophysis on one side in one specimen of *Tympanuchus* and on both sides in another specimen. One specimen of *Pedioecetes phasianellus jamesi* has five synsacro-lumbar vertebrae and the others have four; all have three synsacro-thoraco-lumbar vertebrae.

NERVES

For each nerve (or plexus) the condition found in most specimens of the Lesser Prairie Chicken (*T. pallidicinctus*) is described first. Following this, variations from the typical *T. pallidicinctus* condition are given for *T. pallidicinctus*, then for *T. cupido* (both subspecies considered together), and finally for *P. p. jamesi*.

***Lumbosacral Plexus*, Figs. 2, 3**

T. pallidicinctus

Description.—Eight spinal nerves contribute to the lumbosacral plexus. These are the second through the ninth synsacral spinal nerves (S2 to S9). The entire ventral ramus of each of these nerves, excepting S2 and S9, contributes to this plexus. The ventral ramus of S2 divides into two branches, only the posterior of which contributes to the plexus; the anterior branch directly innervates muscles of the abdominal wall (as does the entire ventral ramus of S1). The ventral ramus of S9 divides into two branches, only the anterior of which contributes to this plexus; the posterior branch contributes to the more posteriorly situated pudendal plexus.

Each root of the plexus corresponds to a single spinal nerve except one spinal nerve (S5—the furcal) that contributes a root to both the femoral nerve and the sciatic nerve; thus typically the plexus has nine roots (but see below). The four anteriormost roots (S2 to S5) contribute to the femoral nerve, although the contribution from S2 is small. S3 and S4 contribute to the obturator nerve. The five posteriormost roots (S5 to S9) contribute to the sciatic nerve, although the contribution from S9 is relatively small.

INDIVIDUAL VARIATION.—In all specimens (of all species) examined, the right and left sides of the plexus in any one individual were practically identical. In T.p. 2 (fig. 2B), there appear to be two furcal nerves; S5 is typical, but a small branch of S4 apparently also contributes to the sciatic nerve. In T.p. 5, S9 is unique in dividing into three branches; the anterior two join the sciatic nerve separately; the posterior one joins the pudendal plexus as usual.

T. cupido

INDIVIDUAL VARIATION.—S2 or S5, or both, may contribute to a limited extent to the obturator nerve. In T.c.p. 3 (fig. 3A) and T.c.a. 1 and 2, much of the plexus has shifted one segment anteriorly, relative to the synsacral vertebrae (the so-called prefixed condition); the roots of the femoral nerve are S2, S3, and S4 (all large); the furcal nerve is S4 (in T.c.a. 1, S5 gives an extremely small root to the femoral nerve, thus making two furcal nerves); six roots (S4 to S9) contribute to the sciatic nerve; S3 and S4 remain as the main contributors to the obturator nerve except in T.c.a. 2 in which only S2 and S3 contribute to it.

P. p. jamesi

INDIVIDUAL VARIATION.—In P.p. 1, the plexus resembles the typical condition in *T. pallidicinctus.* In P.p. 2, 3, and 4, the plexus is prefixed. P.p. 2 resmbles T.c.p. 3. In P.p. 3 and 4 (fig. 3B) there are two furcal nerves (S4 and S5); S2 to S4 are the main contributors to the femoral nerve; only S2 and S3 contribute to the obturator nerve; S4 to S9 contribute to the sciatic nerve (the anteriormost and posteriormost roots are small).

Femoral Nerve, Figs. 4, 5

T. pallidicinctus

DESCRIPTION.—The femoral nerve is short, dividing inside the pelvis into six major divisions—anterior, middle, posterior, anterodorsal, dorsal, and posterodorsal. The anterodorsal and posterodorsal divisions are short, failing to extend so far laterally as the inguinal ligament; the posterodorsal division is also small and is usually covered by other divisions and is not visible when viewed from the ventral side.

The anterior division passes ventral to Mm. iliotrochantericus medius and iliacus and dorsal to the anterior end of the inguinal ligament. The division branches into two parts. The anterior part extends around the posterior border of M. extensor iliotibialis anticus and sends several twigs to the lateral surface of this muscle. The posterior part passes between the proximal parts of Mm. extensor iliotibialis anticus and extensor iliotibialis lateralis and supplies the skin.

The middle division passes ventral to Mm. iliotrochantericus medius and iliacus and dorsal to the inguinal ligament. The division branches into a large but variable number of parts. A variable number of branches (usually two) pass posterior to M. extensor iliotibialis anticus and penetrate the medial surface of M. extensor iliotibialis lateralis. Several branches supply the fused Mm. vastus lateralis and vastus medialis. The posteriormost branch of this division passes between Mm. ambiens and vastus medialis.

giving twigs to the lateral surface of M. ambiens, and sometimes also to the medial surface of M. vastus medialis, and terminates in M. femoritibialis internus.

The posterior division, which does not subdivide, spirals completely around M. psoas (passing in turn anterior, dorsal, posterior, and ventral to it) and gives twigs into this muscle. This nerve then extends distally into the proximal part of the shank and there has a nonmuscular termination.

The short, thick anterodorsal division, partly covered by the anterior division, turns dorsally and passes through the femoral notch of the ilium and penetrates the deep surface of M. gluteus profundus.

The slender dorsal division passes ventral to M. iliotrochantericus medius and dorsal to the inguinal ligament and penetrates the ventral surface of M. iliacus.

The small, short posterodorsal division penetrates the ventral surface of M. iliotrochantericus medius.

Individual Variation.—In two legs the anterior division gives a twig or two twigs to M. extensor iliotibialis lateralis. The dorsal division may fuse proximally with either the anterior or middle division, thus appearing to be a branch of one of these divisions. In one leg (fig. 5A), there are two separate branches (both fused with the middle division) to M. iliacus. On both sides of one specimen (fig. 5A), the anteriormost branch of the middle division, which supplies M. extensor iliotibialis lateralis, gives off a twig that anastomoses with the branch of the anterior division that supplies M. extensor iliotibialis anticus. On both sides of another specimen, the anterodorsal division passes lateral to the anterior end of M. iliotrochantericus medius instead of through the femoral notch, which is lacking.

T. cupido

Individual Variation.—In three legs, the anterior division gives twigs into M. extensor iliotibialis lateralis. The dorsal division is fused proximally with the middle division in one instance. In three cases, a twig from the middle division anastomoses with the branch of the anterior division supplying M. extensor iliotibialis anticus. In the example shown in fig. 5B, a twig comes off the cutaneous branch of the anterior division, perforates the ventral part of M. iliacus, and rejoins the cutaneous branch. In both legs of one specimen, the cutaneous branch of the anterior division perforates the anterior edge of M. extensor iliotibialis lateralis instead of passing between the latter and M. extensor iliotibialis anticus. The posteriormost branch of the middle division, which terminates in M. femoritibialis internus, perforates the medial part of M. vastus medialis in one leg. In another leg, one of the branches to the fused Mm. vastus lateralis and vastus medialis sends a twig into M. extensor iliotibialis lateralis.

P. p. jamesi

Individual Variation.—In three legs, the anterior branch of the anterior division is cutaneous and the posterior branch supplies M. extensor iliotibialis anticus. The dorsal division may fuse proximally with either the anterior or middle division. In one leg (fig. 4B), there are two branches to M. iliacus, one associated with the anterior division and one with the middle division.

Obturator Nerve

T. pallidicinctus

DESCRIPTION.—The long slender obturator nerve passes along the oblique iliac crest and divides into several branches immediately before reaching the obturator foramen. One or two branches, which do not pass through the foramen, penetrate the superficial surface of M. obturator pars postica. Several small branches (variable in number and arrangement) pass through the obturator foramen and supply pars ventralis, pars dorsalis, and pars antica of M. obturator. When pars ventralis and pars dorsalis are fused, one branch perforates the proximal end of this mass and reaches pars antica. One large branch passes through the obturator foramen dorsal to the tendon of M. obturator pars postica, then turns ventrally, passing lateral to the latter; the branch passes between Mm. adductor superficialis and adductor profundus and gives twigs to each of these two muscles.

INDIVIDUAL VARIATION.—None of significance in any of the three species.

Sciatic Nerve, Figs. 6, 7, 8, 9

T. pallidicinctus

DESCRIPTION.—The sciatic nerve passes through the anterior part of the ilio-ischiatic fenestra. Several branches diverge from the nerve immediately after it emerges from the fenestra. The main trunk of the nerve then extends distally through the thigh deep to M. extensor iliofibularis and superficial (lateral) to Mm. flexor ischiofemoralis, caudofemoralis, adductor superficialis, and femorocruralis. The main trunk subdivides into two large nerves—peroneal and tibial—that are adjacent and bound to each other throughout the thigh; the peroneal nerve lies anterior to the tibial. At the distal end of the thigh the main trunk splits grossly into two large branches that diverge and enter the shank. This division does not represent the separation between peroneal and tibial nerves, as is sometimes assumed; the anterior branch includes a part of the tibial nerve as well as the entire peroneal nerve.

A longitudinal groove is visible grossly on the lateral surface of the main trunk, except at the proximal end; distally a second groove is visible posterior to the first one (fig. 6). The long anterior groove indicates the boundary between the peroneal and tibial nerves; this groove may disappear distally, although the posterior groove is always visible distally. The posterior groove, which is continuous with the division of the sciatic nerve into anterior and posterior branches, represents the boundary between two divisions of the tibial nerve. (This is discussed in detail below.) In the middle of the thigh the peroneal and tibial nerves are enclosed in separate connective tissue sheaths, although the two sheaths are fused together; the point of fusion is marked by the anterior groove. If the two sheaths are slit open, the two nerves can be removed and can be seen to be entirely separate. In the proximal part of the main trunk the peroneal and tibial components are enclosed in a single sheath and appear as an undivided trunk; but if the sheath is removed, the two components can be pulled apart rather easily, although there may be some intermingling of a few fibers. This separation can be extended to a point proximal to the origin of all the branches of the sciatic nerve; thus it can be determined which branches arise from the

peroneal component and which from the tibial. (These branches arise from the sciatic nerve as, or immmediately before, the nerve passes through the ilio-ischiatic fenestra; since this level of the intact nerve could not be adequately observed, it was necessary to cut the nerve inside the pelvis and pull the intrapelvic part of the nerve out through the ilio-ischiatic fenestra. In doing this, care had to be taken to avoid damaging the most proximal branches.)

Three main branches arise from the peroneal component (apart from the main trunk) and two from the tibial. Including the peroneal and tibial components of the main trunk, the sciatic nerve can be divided into seven major divisions—anterior peroneal, middle peroneal, dorsal peroneal, posterior or main peroneal (contributes to main trunk), anterior or main tibial (contributes to main trunk), middle tibial, and posterior tibial. Farther distally, the posterior peroneal division becomes the peroneal nerve and the anterior tibial division becomes the tibial nerve. For descriptive purposes, the term peroneal (or tibial) *nerve* will be applied only where the nerve is enclosed in its own sheath, but regardless of whether or not the sheath is fused with another; proximal to this, where the separation may not be precise, the terms peroneal (or tibial) *division* or *component* will be used.

The small anterior peroneal division arises from the anterior edge of the sciatic nerve. Immediately after emerging from the ilio-ischiatic fenestra, the division turns anteriorly and passes deep to M. piriformis, to which the division gives a twig (in some cases more than one twig), then continues forward to supply the posterior part of M. gluteus profundus.

The middle peroneal division branches into two parts. One part penetrates the deep surface of the anteroproximal part of M. extensor iliofibularis. The other part emerges between the proximal ends of Mm. extensor iliofibularis and vastus lateralis and penetrates the deep surface of M. extensor iliotibialis lateralis.

The dorsal peroneal division arises from the posterodorsal part of the peroneal component, then angles posteriorly, crossing the dorsal surface of the anterior tibial division and superficially appears to arise from the tibial component. The dorsal peroneal division usually subdivides into two unequal branches, both of which penetrate the deep surface of the proximal end of M. extensor iliofibularis.

The large middle tibial division soon subdivides into two branches that pass posterodistally lateral to M. flexor ischiofemoralis. One branch (usually the anterior one) passes lateral to M. caudofemoralis (both heads) and emerges between Mm. extensor iliofibularis and flexor cruris lateralis and enters the skin. The other branch passes deep to M. caudofemoralis pars iliofemoralis, and divides into several branches. Several tiny branches penetrate the deep surface of M. caudofemoralis pars iliofemoralis. Another branch also enters the substance of the latter and emerges from the ventral edge of it, giving a twig to pars caudifemoralis, then passes lateral to pars caudifemoralis and enters M. flexor cruris lateralis. Still another branch passes deep to both heads of M. caudofemoralis and enters the anterior part of M. flexor cruris medialis.

The small posterior tibial division arises from the posterior edge of the sciatic nerve. The division diverges from the remainder of the nerve, as the

latter passes through the ilio-ischiatic fenestra, and penetrates the dorsal surface of M. flexor ischiofemoralis.

Below the middle of the main trunk a bundle of fibers of moderate size separates from the anterior edge of the tibial nerve, leaves the tibial sheath, and enters its own sheath, lying superficially between the tibial and peroneal sheaths (fig. 6). At the distal end of the thigh the sheath enclosing this bundle of fibers remains fused with the posterior edge of the peroneal nerve and passes with the latter (diverging from the remainder of the tibial nerve) through the tendinous guide loop for M. extensor iliofibularis, and then diverges from the peroneal nerve. Since this bundle of fibers is distributed with the peroneal nerve, and since the origin of the bundle may be easily overlooked, it has sometimes been misinterpreted as a branch of the peroneal nerve, whereas it almost certainly is a branch of the tibial nerve; this bundle will here be termed the paraperoneal branch of the tibial nerve.

A small but long branch separates from the posterior edge of the proximal end of the tibial nerve or from the tibial component proximal to this and extends distally for some distance adjacent to the tibial nerve, then passes posterodistally between Mm. extensor iliofibularis and flexor cruris lateralis and supplies the skin.

A small branch separates from the anterior edge of the peroneal nerve a short distance above the distal end of the main trunk and passes distolaterally between Mm. extensor iliotibialis lateralis and extensor iliofibularis and supplies the skin.

A twig comes off the medial surface of the tibial nerve near the distal end of the main trunk, passes anteriorly deep to the peroneal nerve, and penetrates the lateral surface of M. femorocruralis; in some cases two twigs enter this muscle.

INDIVIDUAL VARIATION.—In one leg (fig. 7), the twig to M. caudofemoralis pars caudifemoralis arises more proximally than usual and perforates pars iliofemoralis independently of the branch to M. flexor cruris lateralis. The nerve supplying M. flexor cruris lateralis does not perforate M. caudofemoralis pars iliofemoralis, but passes deep to it in three legs. In half the legs, the paraperoneal branch of the tibial nerve, after extending a short distance in its own sheath, enters the sheath of the peroneal nerve and appears grossly to unite with it; if, however, the sheath is slit open, the paraperoneal branch can be easily pulled apart from the posterior edge of the peroneal nerve; the paraperoneal branch is again enclosed in its own sheath at the distal end of the thigh. In one leg, the cutaneous branch of the peroneal nerve perforates the posteroproximal part of M. gastrocnemius pars externa; in three others, this branch is absent. In one of these last three legs (fig. 7), the distal cutaneous branch of the tibial nerve is also absent. In three legs (of different specimens), a minute twig from the middle tibial division passes posteriorly deep to M. caudofemoralis pars caudifemoralis toward the tail (fig. 7); this twig joins the pudendal plexus in one leg; in the other two the twig could not be traced to its termination. Minute twigs come off the peroneal nerve near the middle of the thigh and enter M. extensor iliofibularis in some legs. In a few cases, a minute nonmuscular twig arises from the peroneal nerve near the distal end of the main trunk and passes anteriorly deep to M. vastus lateralis pars postica (fig. 7).

T. cupido

Individual Variation.—In several legs, the nerve supplying M. flexor cruris lateralis does not perforate M. caudofemoralis pars iliofemoralis, but passes deep to it. The branch to M. flexor cruris medialis arises from the posterior (rather than the middle) tibial division in one instance (fig. 8). In one leg, a minute twig from the middle tibial division passes posteriorly and joins the pudendal plexus; in another, a similar twig is present but could not be traced to its termination. In some specimens, minute twigs come off the peroneal nerve near the middle of the thigh and enter M. extensor iliofibularis. In one leg, a nonmuscular twig arises from the base of the cutaneous branch of the peroneal nerve and passes anteriorly deep to M. vastus lateralis pars postica. In another leg (fig. 8), a tiny additional twig arises from the posterior edge of the tibial nerve and subdivides, one branch joining the cutaneous branch of the middle tibial division and the other joining the distal cutaneous branch of the tibial nerve.

P. p. jamesi

Individual Variation.—In both legs of one specimen, the branch to M. flexor cruris medialis arises from the posterior (rather than the middle) tibial division; in three legs, this branch arises as an independent division of the tibial nerve (fig. 6). (Only in one leg does this branch arise as in *T. pallidicinctus*.) The branch to M. flexor cruris medialis perforates the lateral part of M. flexor ischiofemoralis in one instance. In all legs except one (nerve possibly destroyed), a second twig to M. flexor ischiofemoralis arises from the branch to M. flexor cruris medialis (fig. 6). In one leg (fig. 9), an additional branch, arising as an independent division of the sciatic nerve, enters M. extensor iliofibularis distal to the point of entrance of the dorsal peroneal division; this extra branch arises posterior (adjacent) to the dorsal peroneal division, but it could not be determined with certainty whether it arises from the peroneal or tibial component. A minute twig from the branch to M. flexor cruris medialis passes posteriorly and joins the pudendal plexus in one leg (fig. 6); in another, a similar twig is present but could not be traced to its termination. In nearly all the legs, minute twigs come off the peroneal nerve near the middle of the thigh and enter M. extensor iliofibularis (fig. 6). In both legs of one specimen, the paraperoneal branch enters the peroneal sheath (although separable from the peroneal nerve). The distal branch to M. femorocruralis gives off a long twig to M. gastrocnemius pars media in one instance (fig. 6).

Peroneal Nerve, Fig. 10

T. pallidicinctus

Description.—The branch that is given off in the thigh has been discussed above. The peroneal nerve passes, with the paraperoneal branch of the tibial nerve, through the guide loop for M. extensor iliofibularis. The peroneal nerve diverges from the paraperoneal branch and passes along the anterior (proximal) edge of the tendon of M. extensor iliofibularis medial to the common tendon of the lateral heads of Mm. flexor perforatus digiti IV

and flexor perforatus digiti II and lateral to the common tendon of the anterolateral heads of Mm. flexor perforatus digiti IV, flexor perforatus digiti II, and flexor perforatus digiti III.

The peroneal nerve soon gives off a spray of branches that supplies the following: femoral head of M. tibialis anticus, tibial head of M. tibialis anticus (branch passes deep to femoral head), M. extensor digitorum longus (branch passes deep to tibial head of M. tibialis anticus), and M. peroneus longus. A part of the nerve may or may not pass through a notch in the proximal end of the lateral head of M. flexor digitorum longus. The nerve then extends distally along the anterolateral edge of the latter muscle and subdivides into two long branches. Gadow (1891) termed these branches the superficial peroneal and the deep peroneal; his terminology will be used here.

The superficial peroneal branch, after giving off, near its proximal end, one or two twigs into M. peroneus brevis, passes lateral to the retinaculum for the tendon of M. tibialis anticus, then across the intratarsal joint lateral to the latter, then lateral to the insertion of M. tibialis anticus, where the branch subdivides. One of the two resulting branches gives one or two twigs into M. extensor brevis digiti IV, then terminates nonmuscularly in the digits. The other branch passes between the main and accessory insertions of M. tibialis anticus and joins the branch of the deep peroneal which supplies M. abductor digiti II. (See next paragraph.)

The deep peroneal branch passes through the retinaculum for the tendon of M. tibialis anticus, lying lateral, then deep, then medial to the latter; it crosses the intratarsal joint medial to the latter. Immediately above the insertion of M. tibialis anticus, the deep peroneal branch divides, one branch passing on each side of the main insertion. The branch passing lateral to the main insertion passes between the latter and the accessory insertion (medial to the latter) and is joined by a branch of the superficial peroneal nerve. This fused branch extends distally between Mm. extensor hallucis longus and extensor brevis digiti IV and medial to M. extensor brevis digiti III, giving twigs into the latter and into M. abductor digiti II before terminating nonmuscularly in the digits. The branch of the deep peroneal nerve that passes medial to the main insertion of M. tibialis anticus gives one or two twigs into the proximal head of M. extensor hallucis longus, then terminates nonmuscularly in the digits.

INDIVIDUAL VARIATION.—In four legs, the branch of the superficial peroneal nerve that usually joins the lateral branch of the deep peroneal nerve is lacking (fig. 10B). In these legs it can be seen that Mm. extensor brevis digiti III and abductor digiti II are supplied by the deep peroneal nerve.

T. cupido

INDIVIDUAL VARIATION.—In two legs, the same branch that gives twigs into the proximal head of M. extensor hallucis longus also sends a twig into the distal head of this muscle (fig. 10C).

P. p. jamesi

INDIVIDUAL VARIATION.—None of significance.

Tibial Nerve, Fig. 11

T. pallidicinctus

Description.—The branches given off in the thigh have been discussed in the account of the sciatic nerve. At the distal end of the thigh the peroneal nerve and the paraperoneal branch of the tibial nerve diverge from the remainder of the tibial nerve and pass through the tendinous guide loop for M. extensor iliofibularis whereas the remainder of the tibial nerve does not. This main part of the tibial nerve immediately divides into three main divisions—lateral, posterior, and medial.

The lateral division passes between Mm. flexor perforatus digiti IV and gastrocnemius pars externa and subdivides into two branches, one of which penetrates the medial surface of M. gastrocnemius pars externa. The other branch passes deep to the latter and sends twigs into the posterior head of M. flexor perforans et perforatus digiti II, then passes deep to the latter and enters M. flexor perforans et perforatus digiti III.

The posterior division sends a branch into the medial head of M. flexor perforatus digiti IV, then passes between the latter and the medial head of M. flexor perforatus digiti III, and extends distally giving off twigs to each of the three heads of M. flexor perforatus digiti IV, to each of the two heads of M. flexor perforatus digiti III, and to each of the three heads of M. flexor perforatus digiti II. The number and arrangement of these twigs is variable.

The medial division passes medial to the medial head of M. flexor perforatus digiti III, sends a twig to the lateral surface of M. gastrocnemius pars media, then passes into the shank musculature between Mm. plantaris and flexor hallucis longus, and sends a branch along the medial edge of M. flexor hallucis longus that gives several twigs into this muscle before terminating nonmuscularly. A small branch extends to M. popliteus, another to M. plantaris, and another to the posterior head of M. flexor digitorum longus. A nonmuscular branch passes between the medial and posterior heads of M. flexor digitorum longus and extends distally deep to this muscle. A long branch gives off near its proximal end a variable number of twigs that pass deep to M. plantaris and enter M. gastrocnemius pars interna; the branch then extends distally along the lateral edge of M. plantaris and terminates nonmuscularly.

The paraperoneal branch diverges from the peroneal nerve, passing medial and then distal to the insertion of M. extensor iliofibularis, whereas the peroneal nerve passes proximal and then lateral to this insertion. The paraperoneal branch passes deep to the lateral heads of Mm. flexor perforatus digiti IV and flexor perforatus digiti II and superficial to the tendon of the anterolateral head of M. flexor perforatus digiti IV and then passes distally along the anterolateral borders of the latter and the lateral head of M. flexor perforatus digiti III and the posterolateral border of M. flexor digitorum longus. This branch is thus separated from the peroneal nerve by M. flexor digitorum longus and by the fibula; the branch passes along the lateral surface of the tibial cartilage, continues lateral to the hypotarsus, then turns medially before extending distally between Mm. abductor digiti IV and flexor hallucis brevis, sending twigs into each of these muscles and a long twig into M. lumbricalis before terminating nonmuscularly.

INDIVIDUAL VARIATION.—In T.p. 3L,R (fig. 11B), an extra branch arises from the tibial nerve as a separate (fourth) division; it enters the medial head of M. flexor perforatus digiti IV and also gives off a twig that anastomoses with the posterior division (left leg) or with the first branch of the posterior division (right leg). In T.p. 3R (fig. 11B), a large extra branch arises from the proximal part of the medial division and passes medial and then deep to the medial head of M. flexor perforatus digiti III, perforates the tendinous part of the medial head of M. flexor perforatus digiti II, and joins the posterior division (lateral to the medial head of M. flexor perforatus digiti III). A similar branch is found in T.p. 3L except that it arises from the proximal part of the posterior (rather than the medial) division. In T.p. 3R (fig. 11B), the branch to M. gastrocnemius pars externa arises so far proximally that it appears as a separate (fifth) division of the tibial nerve. In two legs, the branch of the medial division that supplies M. gastrocnemius pars media sends a twig into the distal end of M. femorocruralis (fig. 11A).

T. cupido

INDIVIDUAL VARIATION.—In one leg, an extra branch of the medial division arises immediately distal to the branch to M. gastrocnemius pars media and enters the proximal end of the medial head of M. flexor perforatus digiti III. In one instance, the branch to M. gastrocnemius pars interna passes through a gap in the origin of M. plantaris rather than distal to the origin of the latter.

P. p. jamesi

INDIVIDUAL VARIATION.—The branch to M. gastrocnemius pars interna gives a minute twig to the deep surface of the free belly of M. plantaris in one leg.

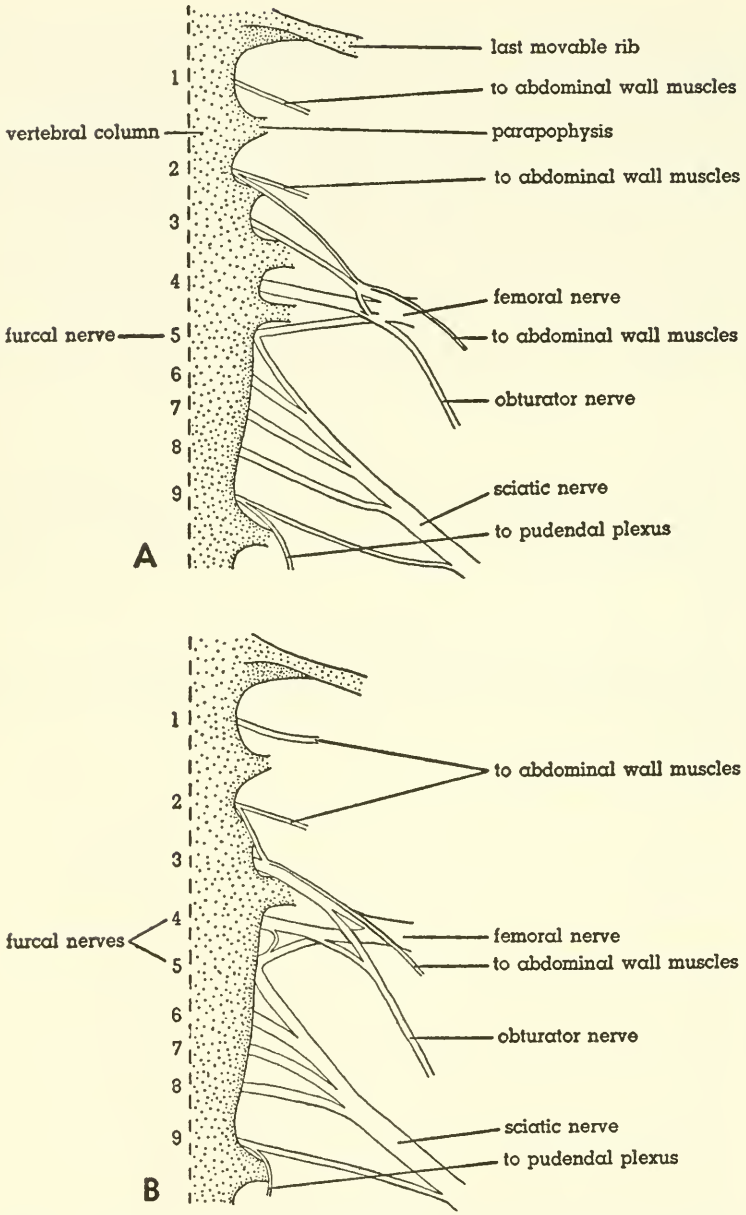


FIG. 2. Ventral views of the lumbosacral plexus of *Tympanuchus pallidicinctus*. Sympathetic ganglionated chain removed. Numbers indicate synsacral spinal nerves. × 2. A. T.p. 1L. B. T.p. 2L.

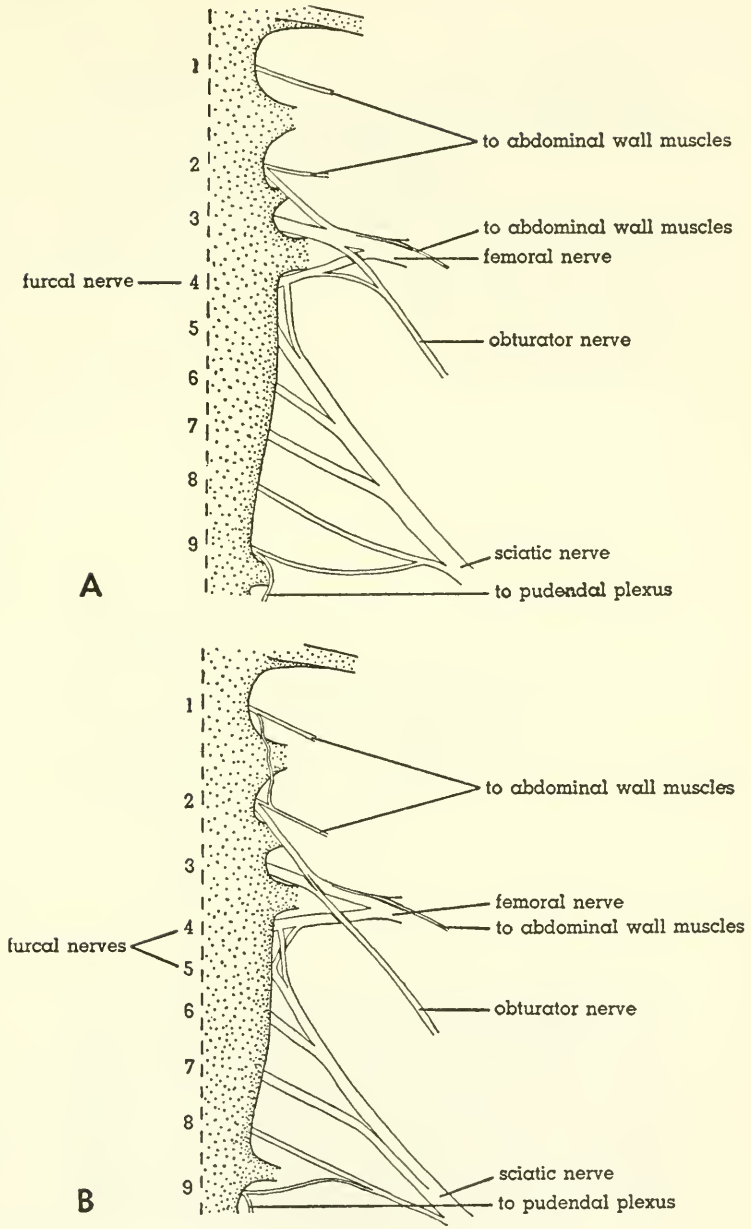


FIG. 3. Ventral views of the lumbosacral plexus. Sympathetic ganglionated chain removed. Numbers indicate synsacral spinal nerves. × 2. A. *Tympanuchus cupido pinnatus* 3L. B. *Pedioecetes phasianellus jamesi* 4L.

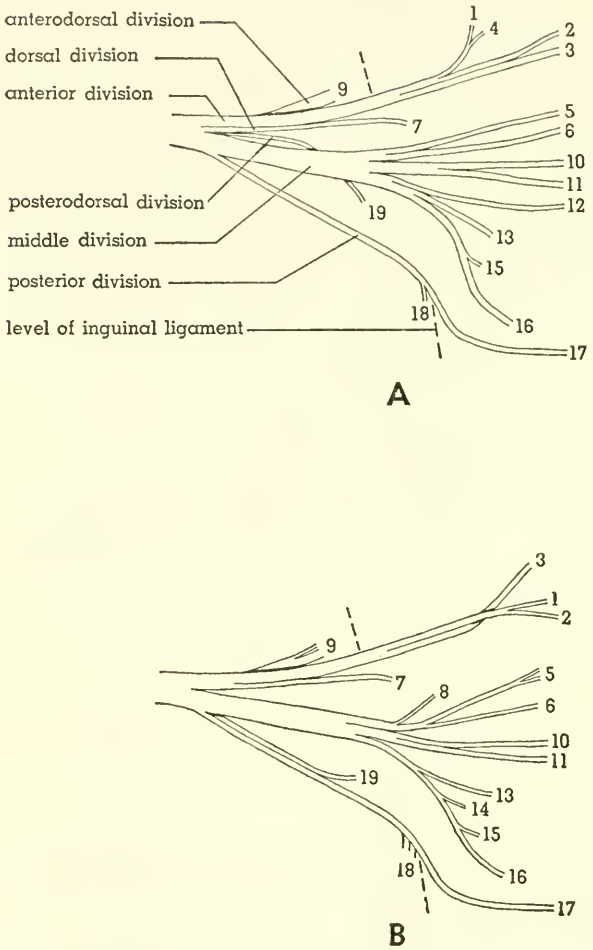
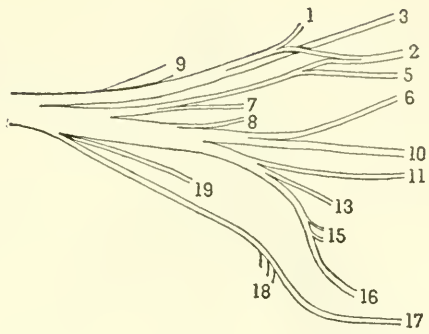
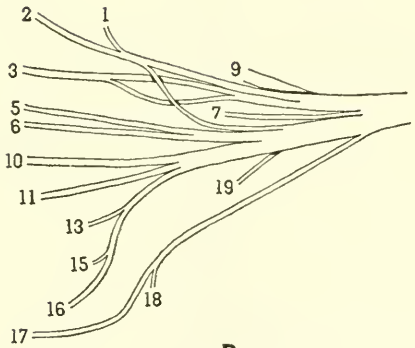


FIG. 4. Semidiagrammatic ventral views of the femoral nerve, showing the distribution of the branches. × 3. 1,2, M. extensor iliotibialis anticus; 3, cutaneous; 4-6, M. extensor iliotibialis lateralis; 7,8, M. iliacus; 9, M. gluteus profundus; 10-12, fused Mm. vastus lateralis and vastus medialis; 13,14, M. vastus medialis; 15, M. ambiens; 16, M. femoritibialis internus; 17, nonmuscular; 18, M. psoas; 19, M. iliotrochantericus medius. A. *Tympanuchus cupido pinnatus* 3L. B. *Pedioecetes phasianellus jamesi* 3L.



A



B

FIG. 5. Semidiagrammatic ventral views of the femoral nerve, showing the distribution of the branches. × 3. 1,2, M. extensor iliotibialis anticus; 3, cutaneous; 5,6, M. extensor iliotibialis lateralis; 7,8, M. iliacus; 9, M. gluteus profundus; 10,11, fused Mm. vastus lateralis and vastus medialis; 13, M. vastus medialis; 15, M. ambiens; 16, M. femoritibialis internus; 17, nonmuscular; 18, M. psoas; 19, M. iliotrochantericus medius. A. *Tympanuchus pallidicinctus* 2L. B. *Tympanuchus cupido attwateri* 1R.

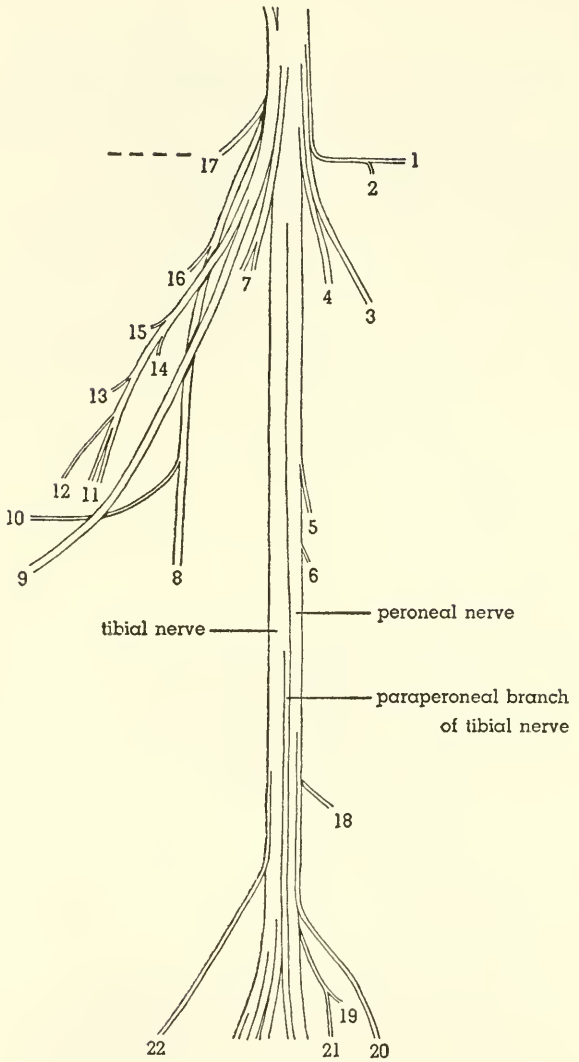


FIG. 6. Semidiagrammatic dorsolateral view of the sciatic nerve of *Pedioecetes phasianellus jamesi* 3R, showing the distribution of the branches. × 2½. 1, M. gluteus profundus; 2, M. piriformis; 3, M. extensor iliotibialis lateralis; 4-7, M. extensor iliofibularis; 8, M. flexor cruris medialis; 9, cutaneous; 10, to pudendal plexus; 11, M. flexor cruris lateralis; 12, M. caudofemoralis pars caudifemoralis; 13-15, M. caudofemoralis pars iliofemoralis; 16,17, M. flexor ischiofemoralis; 18,19, M. femorocruralis (branch of tibial nerve); 20, cutaneous; 21, M. gastrocnemius pars media (branch of tibial nerve); 22, cutaneous.

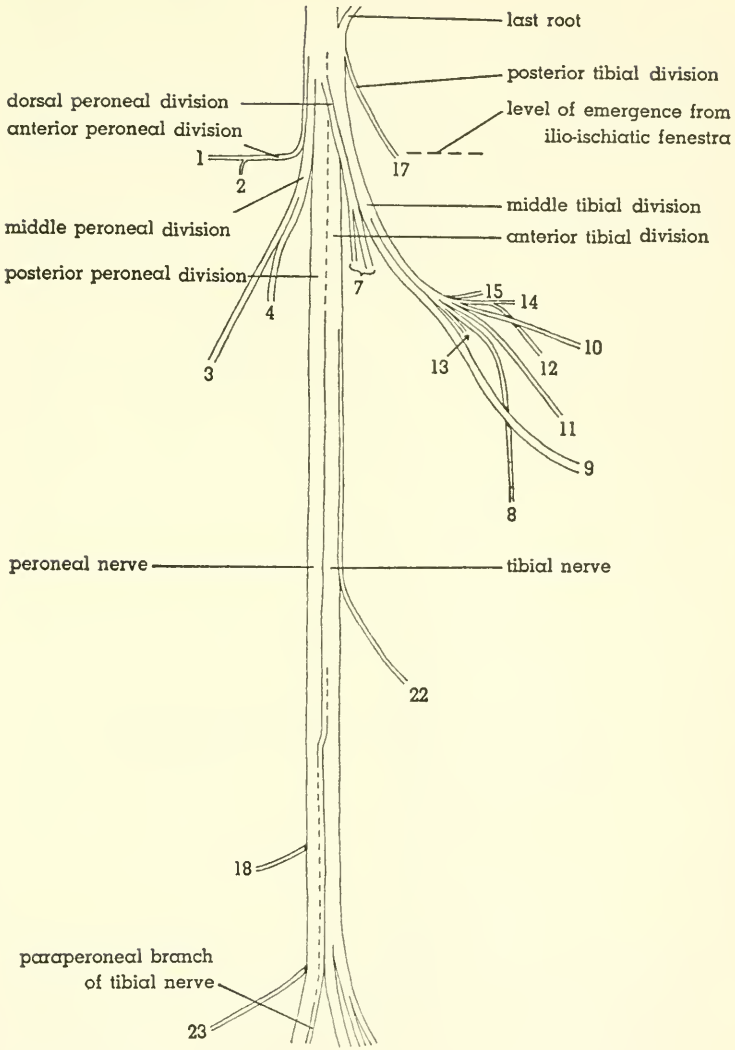


FIG. 7. Semidiagrammatic dorsolateral view of the sciatic nerve of *Tympanuchus pallidicinctus* 2L, showing the distribution of the branches. × 2½. 1, M. gluteus profundus; 2, M. piriformis; 3, M. extensor iliotibialis lateralis; 4,7, M. extensor iliofibularis; 8, M. flexor cruris medialis; 9, cutaneous; 10, to pudendal plexus; 11, M. flexor cruris lateralis; 12, M. caudofemoralis pars caudifemoralis; 13-15, M. caudofemoralis pars iliofemoralis; 17, M. flexor ischiofemoralis; 18, M. femorocruralis (branch of tibial nerve); 22, cutaneous; 23, nonmuscular (branch of peroneal nerve).

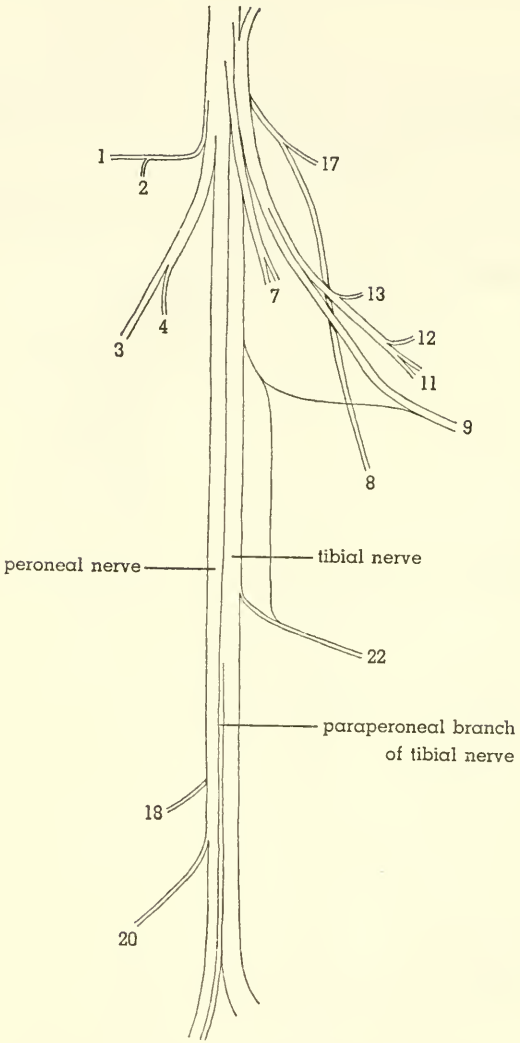


FIG. 8. Semidiagrammatic dorsolateral view of the sciatic nerve of *Tympanuchus cupido pinnatus* 3L, showing the distribution of the branches. × 2½. 1, M. gluteus profundus; 2, M. piriformis; 3, M. extensor iliotibialis lateralis; 4,7, M. extensor iliofibularis; 8, M. flexor cruris medialis; 9, cutaneous; 11, M. flexor cruris lateralis; 12, M. caudofemoralis pars caudifemoralis; 13, M. caudofemoralis pars iliofemoralis; 17, M. flexor ischiofemoralis; 18, M. femorocruralis (branch of tibial nerve); 20, cutaneous; 22, cutaneous.

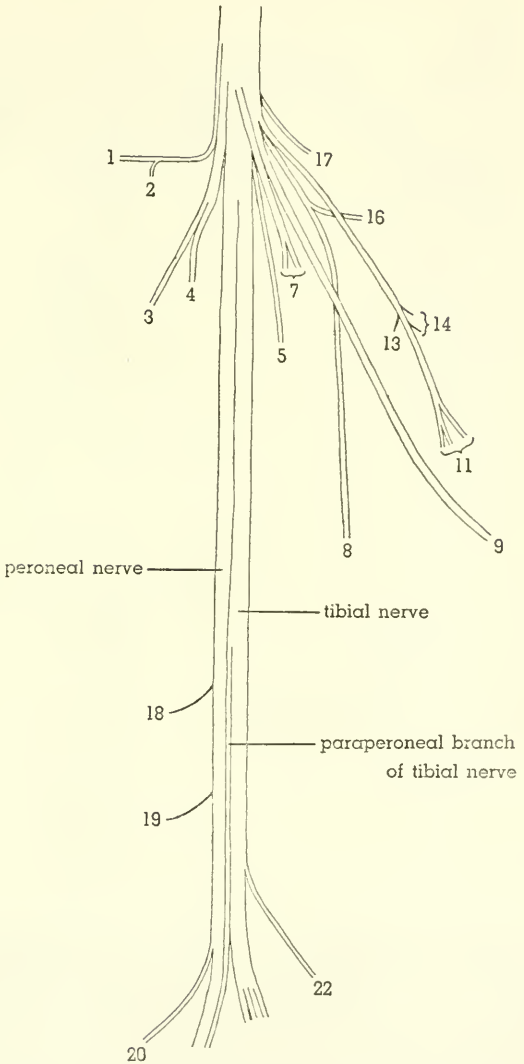


FIG. 9. Semidiagrammatic dorsolateral view of the sciatic nerve of *Pedioecetes phasianellus jamesi* 3L, showing the distribution of the branches. × 2½. 1, M. gluteus profundus; 2, M. piriformis; 3, M. extensor iliotibialis lateralis; 4,5,7, M. extensor iliofibularis; 8, M. flexor cruris medialis; 9, cutaneous; 11, M. flexor cruris lateralis; 13,14, M. caudofemoralis pars iliofemoralis; 16,17, M. flexor ischiofemoralis; 18,19, M. femorocruralis (branch of tibial nerve); 20, cutaneous; 22, cutaneous.

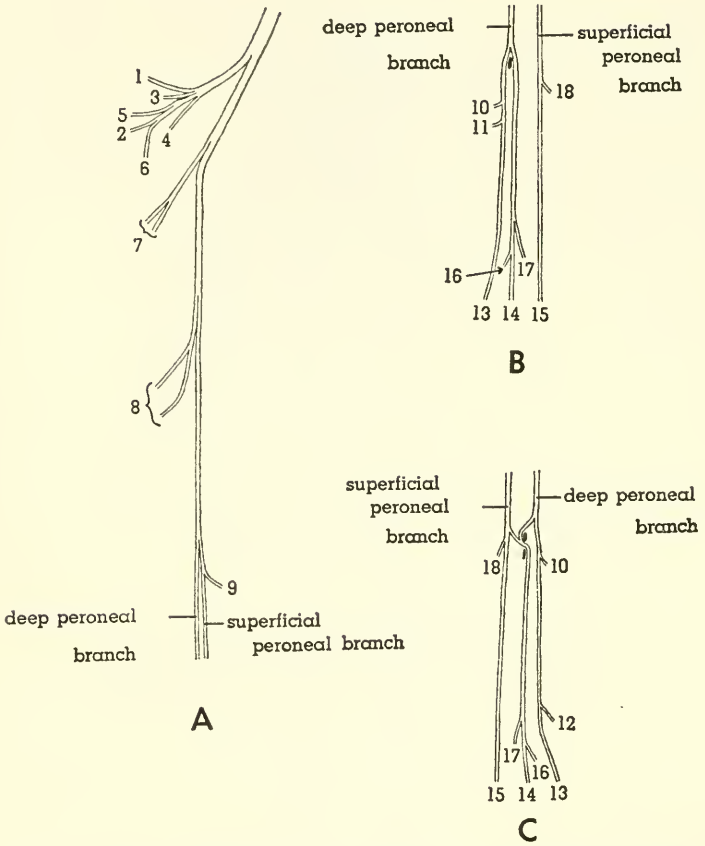


FIG. 10. A,B. Semidiagrammatic drawings of the peroneal nerve of *Tympanuchus pallidicinctus* 1L, showing the distribution of the branches. × 2. C. Semidiagrammatic drawing of the distal part of the peroneal nerve of *Tympanuchus cupido attwateri* 1R, showing the distribution of the branches. × 2. 1,2, M. tibialis anticus (tibial head); 3,4, M. tibialis anticus (femoral head); 5, M. extensor digitorum longus; 6, nonmuscular; 7,8, M. peroneus longus; 9, M. peroneus brevis; 10,11, M. extensor hallucis longus (proximal head); 12, M. extensor hallucis longus (distal head); 13-15, nonmuscular (to toes); 16, M. abductor digiti II; 17, M. extensor brevis digiti III; 18, M. extensor brevis digiti IV.

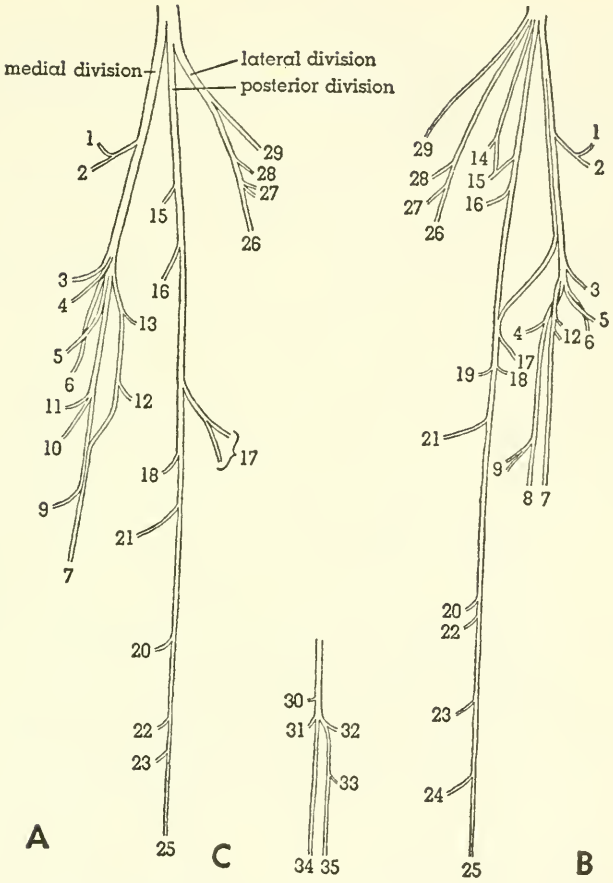


FIG. 11. A,B. Semidiagrammatic drawings of the tibial nerve (excluding the paraperoneal branch) of *Tympanuchus pallidicinctus,* showing the distribution of the branches. × 2. A. T.p. 1L. B. T.p. 3R. C. Semidiagrammatic drawing of the distal part of the paraperoneal branch of the tibial nerve of *Pediocecetes phasianellus jamesi* 2L, showing the distribution of the branches. × 2. 1, M. femorocruralis; 2, M. gastrocnemius pars media; 3, M. popliteus; 4, M. plantaris; 5, M. flexor digitorum longus; 6-8, nonmuscular; 9-11, M. gastrocnemius pars interna; 12,13, M. flexor hallucis longus; 14-16, M. flexor perforatus digiti IV (medial head); 17, M. flexor perforatus digiti III (medial head); 18-20, M. flexor perforatus digiti II; 21, M. flexor perforatus digiti IV (lateral head); 22-24, M. flexor perforatus digiti IV (anterolateral head); 25, M. flexor perforatus digiti III (anterolateral head); 26, M. flexor perforans et perforatus digiti III; 27,28, M. flexor perforans et perforatus digiti II; 29, M. gastrocnemius pars externa; 30,31, M. abductor digiti IV; 32,33, M. flexor hallucis brevis; 34,35, nonmuscular (to toes).

MUSCLES

In the accounts of the muscles the name used by Hudson, *et al.* (1959) for each muscle is given in parentheses after the name used by me if the two differ.

In the account of each muscle, the description of the condition found in most specimens of the Lesser Prairie Chicken (*T. pallidicinctus*) is given first. This is hereafter referrred to as the typical condition for *T. pallidicinctus.* Then any individual variations found within this species are given. Under the heading *T. cupido* any constant differences between this species and typical *T. pallidicinctus* are given first, and any individual variations found within the species *T. cupido* (both subspecies considered together) are given second. Under the heading *P. p. jamesi* any constant differences between this subspecies and the typical condition for *T. pallidicinctus* (thus these differences are not necessarily constant between the two genera) are given first, and any individual variations found within the subspecies *P. p. jamesi* are given second.

In the bird embryo, according to the studies of Romer (1927) and Wortham (1948), the muscles within each segment of the leg differentiate from distinct dorsal or ventral mesenchymal masses. Presumably these represent the primitive dorsal extensor and ventral flexor muscle masses. The list below indicates the ontogenetic origin of the avian leg muscles, according to the studies of Romer and Wortham. The individual muscles are discussed in the order in which they are listed below.

Dorsal muscles of thigh

M. extensor iliotibialis lateralis
M. extensor iliotibialis anticus
M. ambiens
M. vastus lateralis
M. vastus medialis
M. femoritibialis internus
M. extensor iliofibularis
M. piriformis
M. gluteus profundus
M. iliacus
M. iliotrochantericus medius
M. psoas

Ventral muscles of thigh

M. flexor cruris lateralis
M. flexor cruris medialis
M. caudofemoralis
M. flexor ischiofemoralis
M. adductor superficialis
M. adductor profundus
M. obturator
M. femorocruralis

Ventral muscles of shank

M. gastrocnemius
M. flexor perforans et perforatus digiti II
M. flexor perforans et perforatus digiti III
M. flexor perforatus digiti IV
M. flexor perforatus digiti III
M. flexor perforatus digiti II
M. flexor hallucis longus
M. plantaris
M. flexor digitorum longus
M. popliteus

Dorsal muscles of shank

M. peroneus longus
M. tibialis anticus
M. extensor digitorum longus
M. peroneus brevis

Dorsal muscles of foot

M. extensor hallucis longus
M. abductor digiti II
M. extensor brevis digiti III
M. extensor proprius digiti III
M. extensor brevis digiti IV

Ventral muscles of foot

M. lumbricalis
M. abductor digiti IV
M. flexor hallucis brevis
(M. adductor digiti II—not present)
(M. adductor digiti IV—not present)

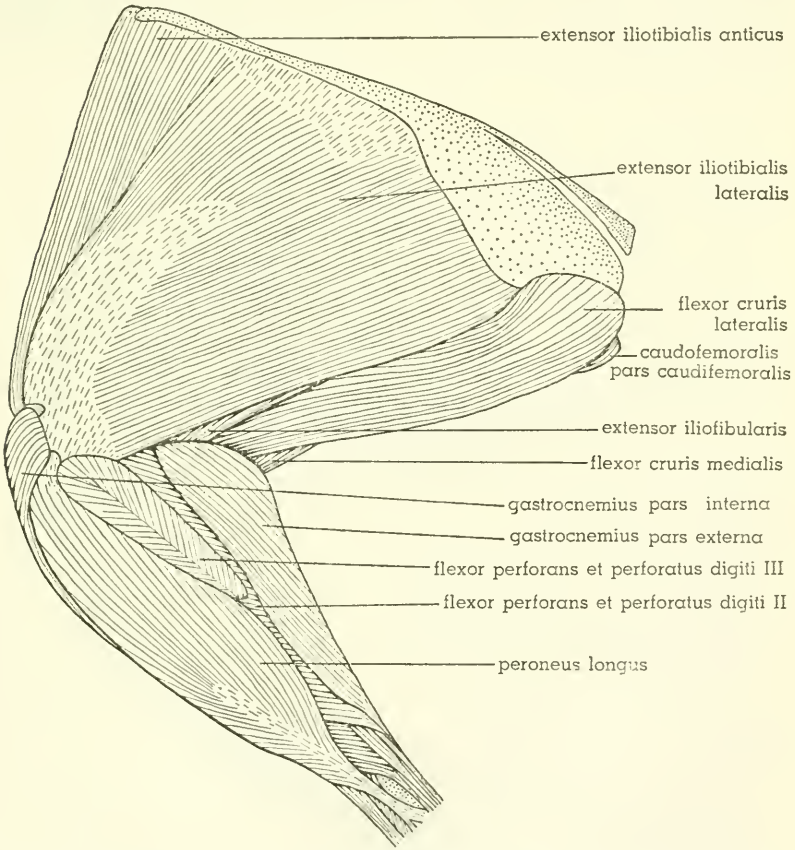


FIG. 12. *Tympanuchus pallidicinctus* 2L. Lateral view of the superficial muscles of the left leg. × 1.

M. Extensor Iliotibialis Lateralis (M. iliotibialis), Figs. 12, 13, 20F, G

T. pallidicinctus

General Description and Relations.—Most superficial muscle on lateral surface of thigh; broad, flat, and triangular; bounded anteriorly by M. extensor iliotibialis anticus and posteriorly by M. flexor cruris lateralis; posterior part considerably thicker than anterior part; anteroproximal and centrodistal parts aponeurotic; extreme posteroproximal corner also aponeurotic (could be considered tough sheet of connective tissue intimately fused with M. extensor iliotibialis lateralis, rather than part of muscle itself; see fig. 20F); latter aponeurosis, as well as adjacent fleshy fibers, overlapped by M. flexor cruris lateralis; this aponeurosis fused with posterior end of underlying M. caudofemoralis pars iliofemoralis; centrodistal aponeurosis tightly fused to underlying Mm. vastus lateralis and vastus medialis; fleshy fibers posterior to this aponeurosis also fused with M. vastus lateralis, although posterior third of

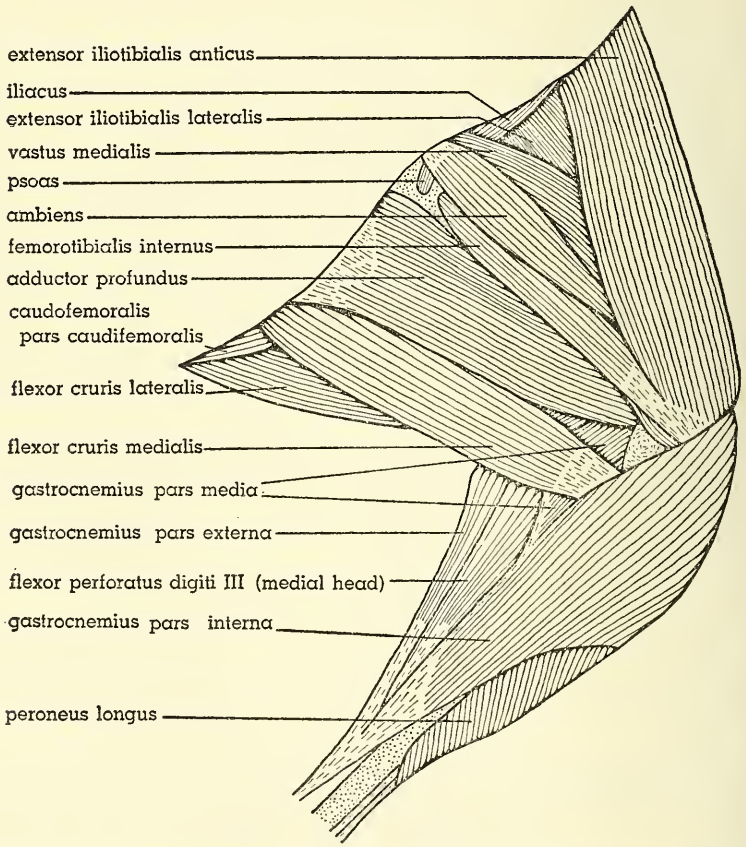


Fig. 13. *Tympanuchus pallidicinctus* 2L. Medial view of the superficial muscles of the left leg. × 1. Articular capsule shown by concentrically arranged dashes.

muscle free; fleshy part anterior to this aponeurosis bound by tough connective tissue to underlying M. vastus medialis, although no fusion of fibers; anterior edge tightly bound by strong connective tissue to M. extensor iliotibialis anticus, with some fusion of fibers (proximally); posteroproximal corner bound by tough connective tissue to adjacent muscles; anteroproximal aponeurosis fused with aponeurotic anteroproximal part of underlying M. extensor iliofibularis. Continuous proximal aponeurosis of M. extensor iliotibialis anticus and of M. extensor iliotibialis lateralis underlain by tough fascial sheet overlying M. gluteus profundus; anterior part of this fascia tightly fused to latter muscle but free from overlying aponeurosis; posterior part of this fascia tightly fused to overlying aponeurosis but free from M. gluteus profundus; middle part of fascia fused to both aponeurosis and M. gluteus profundus.

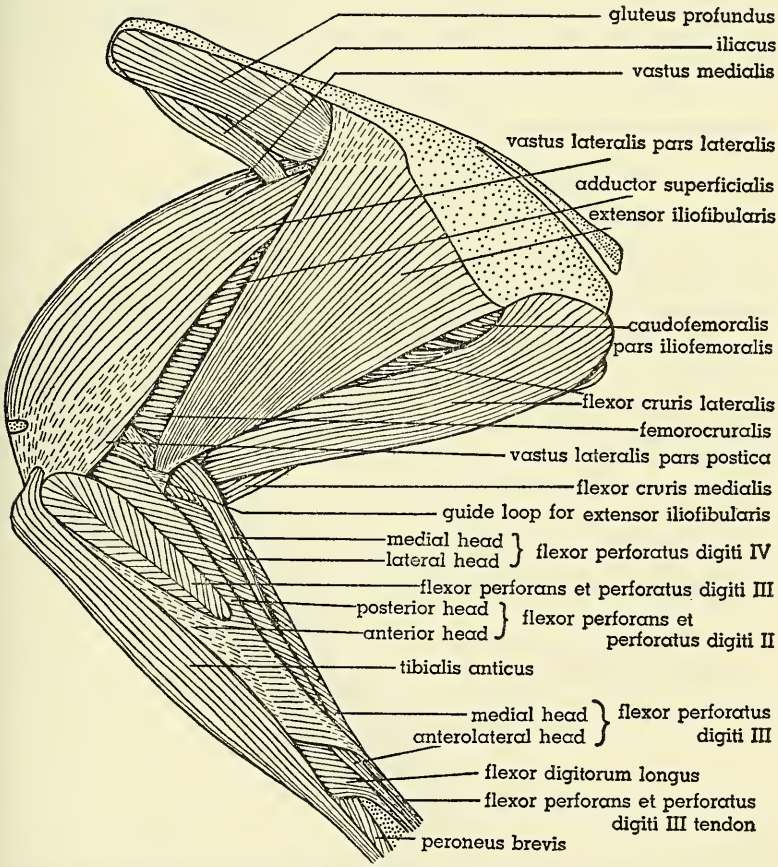


FIG. 14. *Tympanuchus pallidicinctus* 2L. Lateral view of the muscles of the left leg. The following muscles have been removed: extensor iliotibialis lateralis, extensor iliotibialis anticus, gastrocnemius pars externa and pars interna, and peroneus longus. × 1.

ORIGIN.—Approximately the anterior half attaches by an extensive aponeurosis, which is continuous anteriorly with that of M. extensor iliotibialis anticus, to the anterior iliac crest, ending posteriorly at the anterior end of the lateral iliac process; the posterior part attaches fleshily to the edge of the entire lateral iliac process and (posterior few mm.) aponeurotically to the entire lateral ischiatc ridge. The proximal part of the belly is much thicker than the fleshy origin. Two accessory aponeuroses associate with the anterior part of the muscle; the proximal one of these comes off the deep surface several mm. distal to the proximal end of the fleshy belly and passes medially between Mm. gluteus profundus and iliacus, fusing to both these muscles, and attaches to the lateral edge of M. iliotrochantericus medius and to the lateral edge of the ilium anterior to the latter; the aponeurosis actually splits into two sheets at the edge of M. iliotrochantericus medius; these sheets fuse to the dorsal and ventral surfaces of the latter muscle, enclosing it; the part of this aponeurosis between Mm. iliacus and iliotrochantericus medius is strongly fused with the underlying body wall. The distal accessory aponeu-

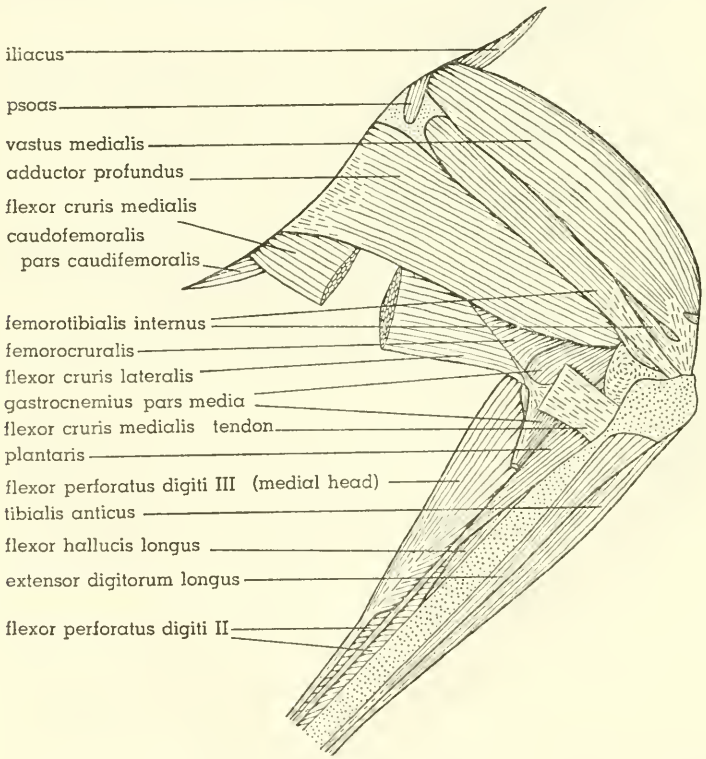


FIG. 15. *Tympanuchus pallidicinctus* 2L. Medial view of the muscles of the left leg. The following muscles have been removed: extensor iliotibialis lateralis, extensor iliotibialis anticus, ambiens, flexor cruris lateralis (in part), flexor cruris medialis (in part), gastrocnemius pars externa and pars interna, and peroneus longus. × 1.

rosis (sometimes weak) comes off the deep surface several mm. distal to the proximal one and passes medially along the ventral surface of M. iliacus, fusing with the latter, then joining the proximal accessory aponeurosis medial to M. iliacus.

INSERTION.—The muscle inserts by a broad aponeurosis strongly fused to the underlying Mm. vastus lateralis and vastus medialis; the aponeurosis contributes superficially to the patellar tendon, attaching to the lateral half of the rotular crest.

INNERVATION.—A variable number of branches (usually two) of the middle division of the femoral nerve pass ventral to M. iliacus and between Mm. extensor iliotibialis anticus and vastus medialis and enter the deep surface of the anteroproximal part of the muscle. The branch of the middle peroneal

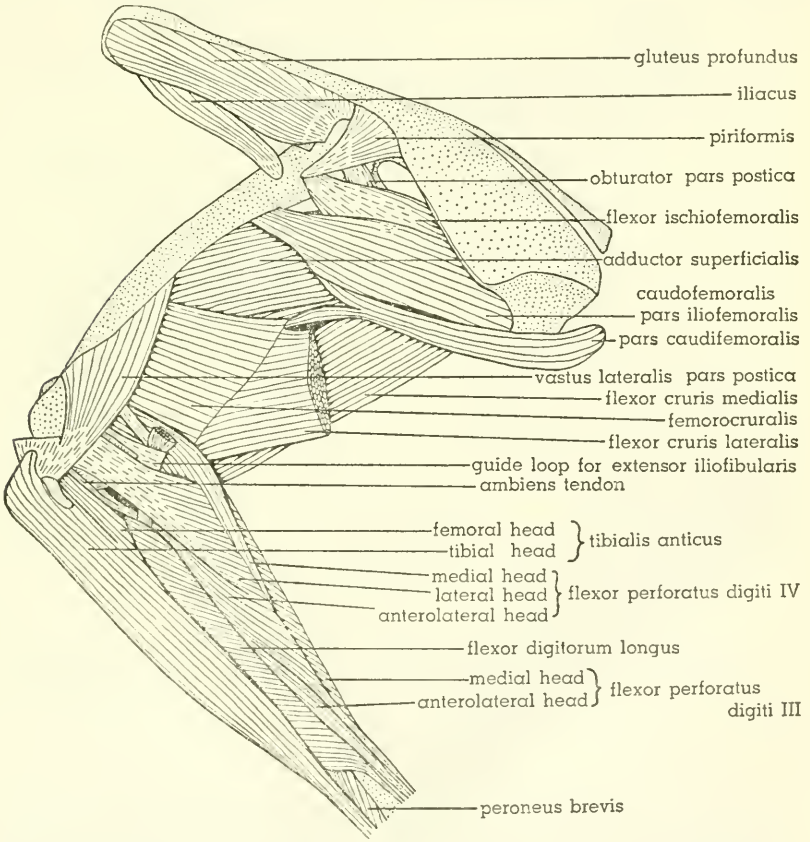


FIG. 16. *Tympanuchus pallidicinctus* 2L. Lateral view of the muscles of the left leg. The following muscles, in addition to those listed for Fig. 14, have been removed: ambiens, vastus lateralis pars lateralis, vastus medialis (except for part of patellar tendon), extensor iliofibularis, flexor cruris lateralis (in part), flexor perforans et perforatus digiti II, and flexor perforans et perforatus digiti III. × 1.

division of the sciatic nerve emerges between the proximal ends of Mm. extensor iliofibularis and vastus lateralis and sends twigs into the deep surface of M. extensor iliotibialis lateralis.

INDIVIDUAL VARIATION.—In two legs, the nerve supplying M. extensor iliotibialis anticus gives twigs into M. extensor iliotibialis lateralis.

T. cupido

DIFFERENCES FROM *T. pallidicinctus*.—The fleshy origin from the lateral iliac process is considerably thicker (reflected in a thicker lateral iliac process).

INDIVIDUAL VARIATION.—In three legs the nerve supplying M. extensor iliotibialis anticus gives twigs into M. extensor iliotibialis lateralis. In another leg one of the branches to the fused Mm. vastus lateralis and vastus medialis sends a twig into M. extensor iliotibialis lateralis.

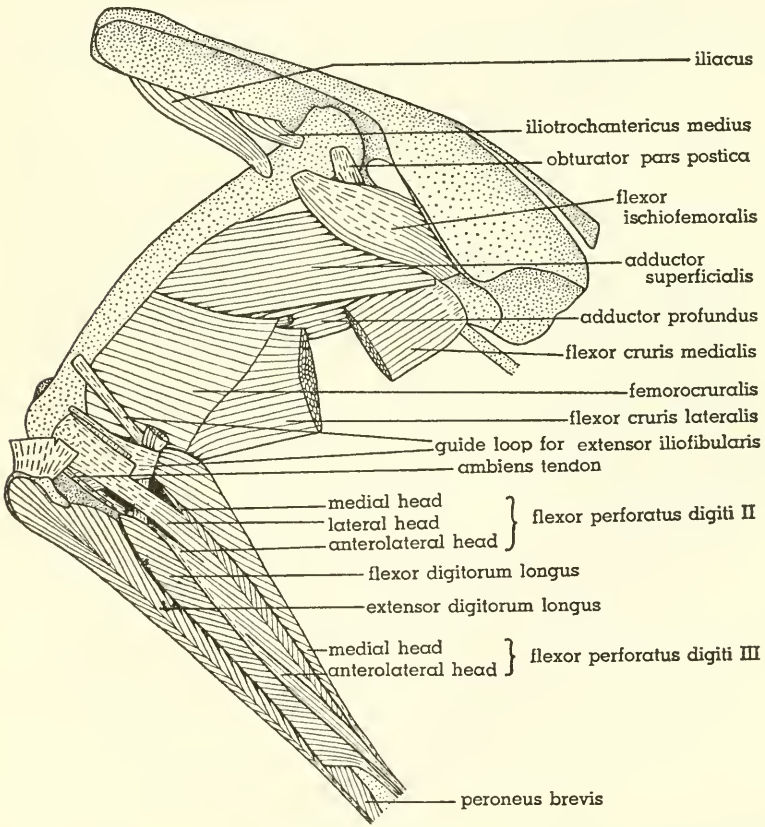


FIG. 17. *Tympanuchus pallidicinctus* 2L. Lateral view of the muscles of the left leg. The following muscles, in addition to those listed for Fig. 16, have been removed: vastus lateralis pars postica, gluteus profundus, flexor cruris medialis (in part), caudofemoralis, flexor perforatus digiti IV, and tibialis anticus. × 1.

P. p. jamesi

DIFFERENCES FROM TYPICAL *T. pallidicinctus*.—The posteroproximal aponeurosis is more extensive, resulting in a narrower proximal fleshy end (fig. 20G); the fleshy fibers adjacent to this aponeurosis are not overlapped by M. flexor cruris lateralis. There is a fusion of fibers between the anterodistal fleshy part of M. extensor iliotibialis lateralis and the underlying M. vastus medialis, but there is no fusion of fibers between the anterior edge of M. extensor iliotibialis lateralis and M. extensor iliotibialis anticus. The connective tissue binding the posteroproximal corner to adjacent muscles is stronger. The fleshy part of the origin is narrower, partly tendinous, and

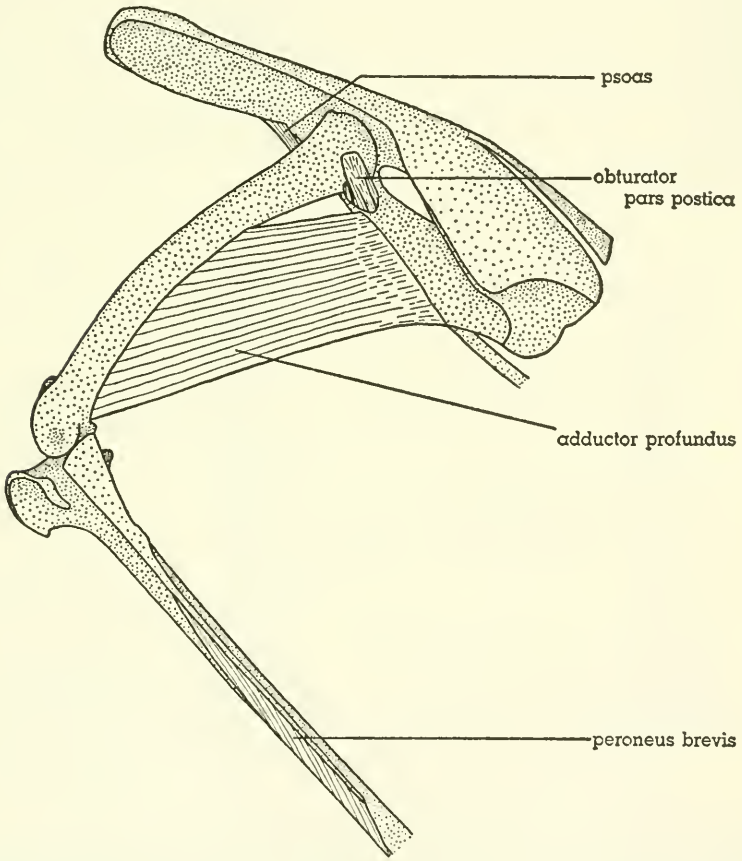


FIG. 18. *Tympanuchus pallidicinctus* 2L. Lateral view of the muscles of the left leg. The following muscles, in addition to those listed for Fig. 17, have been removed: patellar tendon, iliacus, iliotrochantericus medius, flexor cruris lateralis, flexor cruris medialis, flexor ischiofemoralis, adductor superficialis, femorocruralis, gastrocnemius pars media, flexor perforatus digiti III, flexor perforatus digiti II, flexor hallucis longus, plantaris, flexor digitorum longus, popliteus, and extensor digitorum longus. × 1.

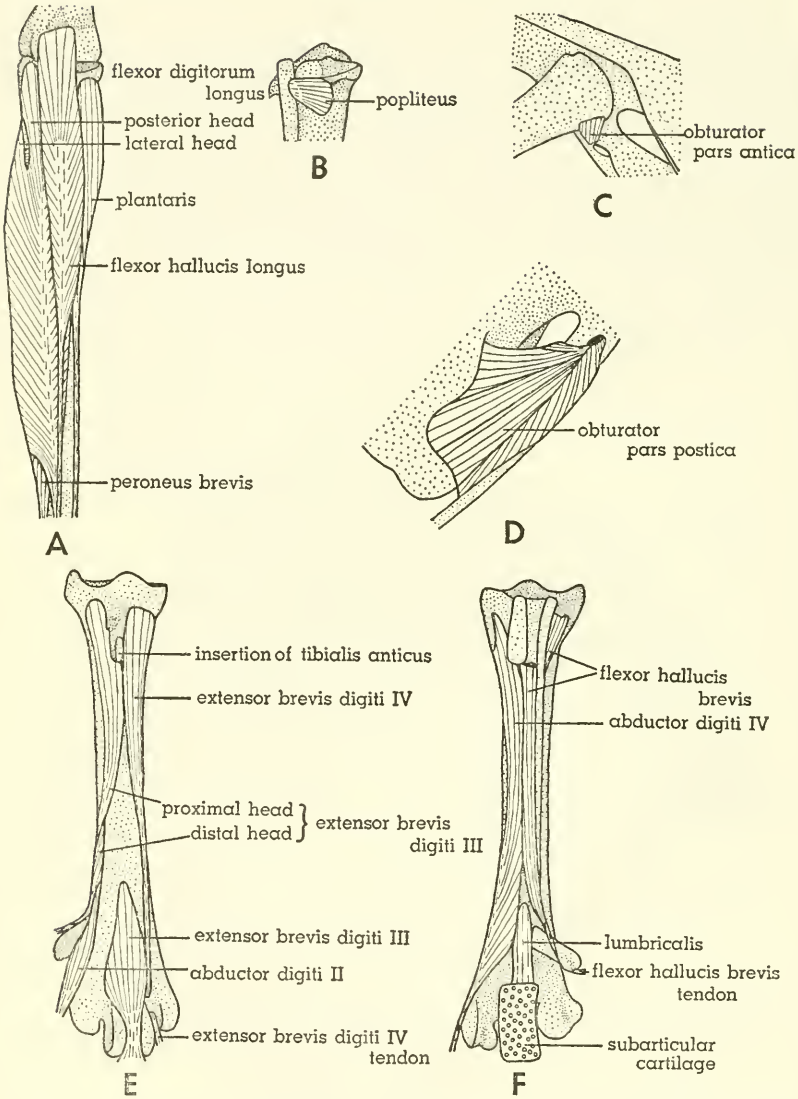


FIG. 19. *Tympanuchus pallidicinctus* 2L. A. Posterior view of the muscles of the left shank. The following shank muscles, in addition to those listed for Fig. 17, have been removed: gastrocnemius pars media, flexor perforatus digiti III, and flexor perforatus digiti II. × 1. B. Posterior view of the proximal end of the shank, showing the most deeply situated muscle. × 1. C. Lateral view of the head of the left femur and the middle part of the pelvis, showing the deepest part of M. obturator. × 1. D. Medial view of the posteroventral part of the left side of the pelvis, showing the intrapelvic part of M. obturator. × 1. E. Anterior view of the left tarsometatarsus, showing the dorsal intrinsic muscles of the foot. × 1½. F. Posterior view of the left tarsometatarsus, showing the ventral intrinsic muscles of the foot. × 1½.

much thinner (reflected in a thin lateral iliac process). The proximal border is much more nearly straight, owing to a less pronounced lateral iliac process. The distal accessory aponeurosis is absent.

INDIVIDUAL VARIATION.—The muscle is usually somewhat fused to the posteroproximal and anteroproximal fleshy corners of the underlying M. extensor iliofibularis.

M. Extensor Iliotibialis Anticus (M. sartorius), Figs. 12, 13

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Anteriormost muscle of thigh; long and strap-shaped; proximal part entirely anterior (adjacent) to M. extensor iliotibialis lateralis; posterior edge of middle part medial to latter muscle; distal part mostly medial to Mm. extensor iliotibialis lateralis and vastus medialis; proximal part aponeurotic, continuous posteriorly with anteroproximal aponeurosis of M. extensor iliotibialis lateralis; anterior edge of M. extensor iliotibialis lateralis bound by strong connective tissue to adjacent part of M. extensor iliotibialis anticus; some fusion of fibers (proximally) between these two muscles; anteroproximal corner of fleshy part of muscle sometimes fused to underlying anterior edge of ilium and fascia covering body wall musculature adjacent (anterior) to ilium.

ORIGIN.—The muscle arises aponeurotically from the anterior part of the anterior iliac crest and (anteroproximal corner) from the anterior end of the median dorsal ridge.

INSERTION.—The flat tendon, continuous posteriorly with the superficial tendon of M. femoritibialis internus, fuses to the tendon of M. vastus medialis, contributing superficially to the medial part of the patellar tendon, which attaches to the medial half of the rotular crest; most of the tendon is overlapped by the edge of M. gastrocnemius pars interna.

INNERVATION.—A branch of the anterior division of the femoral nerve gives twigs into the lateral surface of the posterior part.

INDIVIDUAL VARIATION.—In two legs, a twig from the anteriormost branch of the middle division of the femoral nerve anastomoses with the typical branch to M. extensor iliotibialis anticus.

T. cupido

INDIVIDUAL VARIATION.—In several legs, the anterior edge of origin extends forward onto the neural spine of the last free thoracic vertebra. A twig from the middle division of the femoral nerve anastomoses with the typical branch to M. extensor iliotibialis anticus in three legs.

P. p. jamesi

DIFFERENCES FROM TYPICAL *T. pallidicinctus*.—There is no fusion of fibers between M. extensor iliotibialis anticus and M. extensor iliotibialis lateralis.

INDIVIDUAL VARIATION.—The anterior edge of origin extends forward onto the neural spine of the last free thoracic vertebra in some legs.

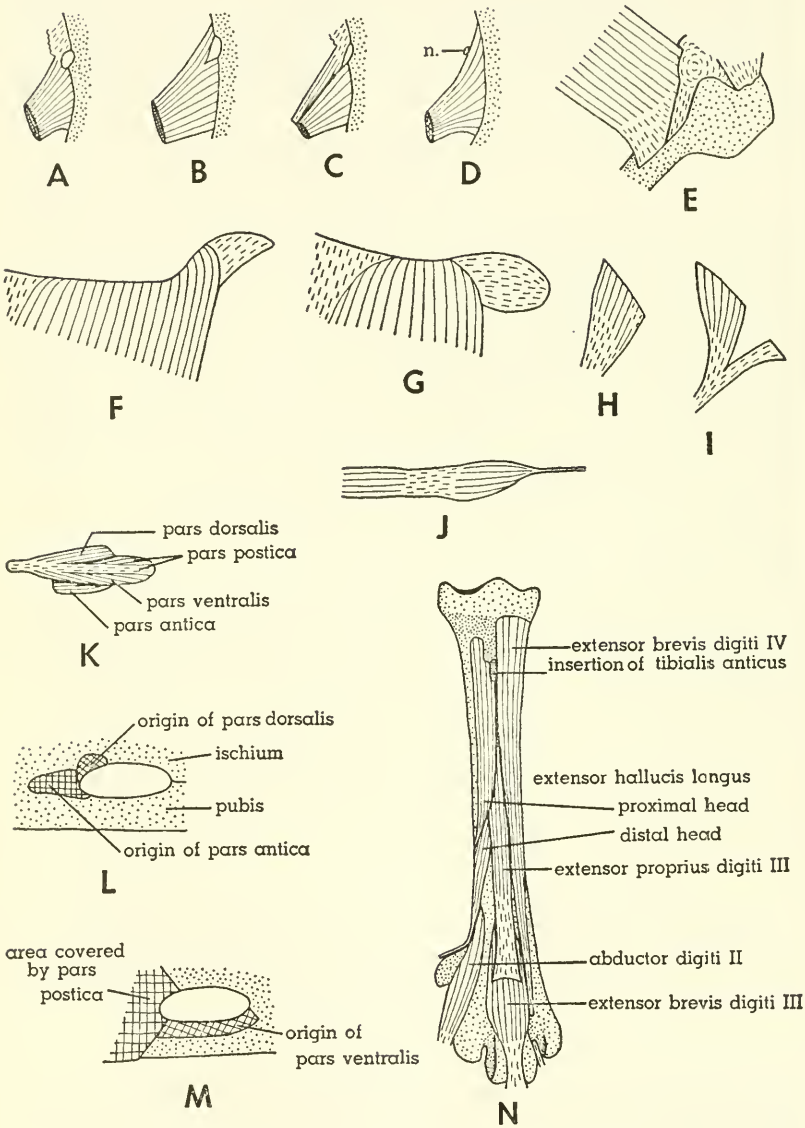


FIGURE 20. Explanation on opposite page.

EXPLANATION OF FIGURE 20

A-D. Dorsal views of M. iliotrochantericus medius, showing its relationship to femoral notch. × 1. In D, note absence of femoral notch and location of branch of femoral nerve. A. *Tympanuchus pallidicinctus* 2L. B. *T. cupido pinnatus* 4L. C. *Pedioecetes phasianellus jamesi* 1L. D. *T. pallidicinctus* 3L.

E. Medial view of distal end of M. flexor cruris medialis of *P. p. jamesi* 4L. × 1. Part of insertion is covered by medial collateral ligament.

F,G. Lateral views of posteroproximal corner of M. extensor iliotibialis lateralis (removed from specimen). × 1. F. *T. pallidicinctus* 2L. G. *P. p. jamesi* 3L.

H,I. Dorsolateral views of M. piriformis. × 1. H. *P. p. jamesi* 1L. I. *T. cupido attwateri* 1L.

J. Lateral view of M. caudofemoralis pars caudifemoralis (removed from specimen) of *T. c. pinnatus* 4L. × 1.

K. Lateral view of extrapelvic part of M. obturator of *T. pallidicinctus* 3L (bones not shown). × 2.

L,M. Region surrounding obturator foramen of *T. pallidicinctus* 3L, showing points of attachment of three parts of M. obturator (muscles removed). × 3. L. Lateral view. M. Medial view.

N. Anterior view of left tarsometatarsus of *P. p. jamesi* 4L, showing dorsal intrinsic muscles of foot. × 1½. Tendon of M. extensor digitorum longus has been removed.

M. Ambiens, Figs. 13, 16, 17

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Thin and elongate; on medial surface of thigh; broadest above middle of belly; belly narrowed distally, forming long slender tendon passing lateral to distal part of M. extensor iliotibialis anticus; bounded anterolaterally by M. vastus medialis and posterolaterally by Mm. femoritibialis internus and psoas (proximally).

ORIGIN.—The muscle arises by a short flat tendon from the pectineal process.

INSERTION.—The long slender tendon enters an elongate channel within the patellar tendon; the point of entrance is at the proximal end of the latter tendon just medial to the patella; the tendon passes distolaterally (within the channel) below the patella and emerges from the distolateral edge of the patellar tendon and then extends distally along the anterolateral surface of the head of the fibula, superficial to the fibular arm of the guide loop for M. extensor iliofibularis, and joins the anterolateral surface of the common tendon of origin of the anterolateral heads of Mm. flexor perforatus digiti III, flexor perforatus digiti IV, and flexor perforatus digiti II; the point of junction is usually immediately proximal to the proximal end of the lateral head of M. flexor digitorum longus.

INNERVATION.—The branch of the middle division of the femoral nerve that supplies M. femoritibialis internus gives off a tiny twig or twigs that penetrate the lateral surface of the proximal part of M. ambiens.

INDIVIDUAL VARIATION.—None of significance in *T. pallidicinctus* or in *P. p. jamesi;* in *T. cupido* the origin is partly fleshy in one leg.

M. Vastus Lateralis (M. femoritibialis externus + part of M. femoritibialis medius), Figs. 14, 16

Fisher and Goodman (1955) apply the name femoritibialis externus to the muscle unit that I here term the pars postica of M. vastus lateralis. The reasons for this change are discussed in the section on terminology.

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Thick; on lateral surface of femur deep to M. extensor iliotibialis lateralis; anterior to M. extensor iliofibularis and lateral to M. vastus medialis; much of lateral surface, except proximal part, fused with overlying M. extensor iliotibialis lateralis; deep surface of anterior half fused with M. vastus medialis; proximal part overlapping, but usually not fusing with, insertions of Mm. iliacus and caudofemoralis; partially separable into two parts—pars lateralis and pars postica, former constituting main part of muscle; latter considerably smaller and situated deep to posterodistal part of pars lateralis, except for posterodistal part extending posterior to edge of pars lateralis; proximal part of pars postica strongly fused with pars lateralis; posterodistal tendinous edge of pars lateralis fused or not fused with lateral surface of pars postica; proximal end (narrow) of pars postica tendinous and variable in length.

ORIGIN.—*Pars lateralis:* This arises fleshily from most of the lateral surface and (distally) from the anterior surface of the femur, extending anteriorly to

the anterior intermuscular line, fusing with M. vastus medialis, and extending posteriorly to the posterolateral intermuscular line (proximally) and the origin of pars postica (distally); the proximal end begins at the level of the distal edge of the insertion of M. iliotrochantericus medius, contacting the insertions of Mm. iliotrochantericus medius, piriformis, and flexor ischiofemoralis, and terminates distally at the level of the proximal ends of the femoral condyles.

Pars postica: This arises fleshily and tendinously (proximal end and deep surface) from the posterolateral surface of approximately the distal half of the femur, extends posteromedially to the posterolateral intermuscular line where it contacts the origin of M. femorocruralis, and extends anteriorly to the level of a line drawn diagonally across the femur from the proximal end of the origin (at the posterolateral intermuscular line) to the proximal end of the external condyle; the distal end is anterior (adjacent) to the attachment of the proximal arm of the tendinous guide loop for M. extensor iliofibularis; the origin is adjacent to, but distinct from, the origin of pars lateralis.

INSERTION.—*Pars lateralis* is fused indistinguishably with M. vastus medialis; these two muscles form the main (middle) part of the patellar tendon, which also receives contributions from pars postica and Mm. femoritibialis internus, extensor iliotibialis lateralis, and extensor iliotibialis anticus; the patellar tendon attaches to the entire rotular crest of the tibia; the patella is situated in the proximal part of this tendon; some deep fleshy fibers of M. vastus lateralis pars lateralis and M. vastus medialis attach to the proximal edge of the patella. *Pars postica* forms a short narrow tendon that fuses to the lateral part of the tendon of pars lateralis, forming the lateralmost part of the patellar tendon. A broad flat vinculum extends from the lateral surface of the femorofibular fascia (defined under M. flexor perforans et perforatus digiti II) to the deep surface of the lateral part of the patellar tendon; a similar vinculum extends from the medial surface of the internal condyle to the deep surface of the medial part of the patellar tendon.

INNERVATION.—Two or more branches of the middle division of the femoral nerve penetrate the anterior surface of the fused Mm. vastus lateralis (pars lateralis) and vastus medialis; short twigs emerge from the deep surface of pars lateralis and penetrate the superficial surface of the anteroproximal part of pars postica.

INDIVIDUAL VARIATION.—The proximal ends of M. vastus medialis and M. vastus lateralis are usually separated by a deep notch. In some legs, a small bundle of fibers forming the anteroproximal part of M. vastus lateralis attaches to the lateral surface of M. vastus medialis anterior to this notch.

T. cupido

INDIVIDUAL VARIATION.—One leg shows the same variation found in *T. pallidicinctus* (see above). In several legs, pars lateralis does not extend so far proximally as usual, but begins at the level of insertion of M. piriformis (does not contact the insertion of M. iliotrochantericus medius) and may not overlap M. iliacus. In a few legs, no vincula are associated with the patellar tendon.

P. p. jamesi

INDIVIDUAL VARIATION.—Pars lateralis often begins proximally at the level of the insertion of M. piriformis.

M. Vastus Medialis (Part of M. femoritibialis medius), Figs. 13, 14, 15

T. pallidicinctus

General Description and Relations.—Thick; on anteromedial surface of femur medial to anterior part of M. vastus lateralis pars lateralis; bounded medially by Mm. ambiens and extensor iliotibialis anticus (distally); bounded posteromedially by M. femortibialis internus; proximal part medial to posterior ends of Mm. iliacus, iliotrochantericus medius, and gluteus profundus; lateral surface, except proximal part, fused with anterior part of M. vastus lateralis pars lateralis; part of lateral surface of M. vastus medialis covered by sheet of fascia attaching to anterior intermuscular line; M. vastus lateralis separable from this fascia, but fascia absent anteriorly and distally and these two muscles indistinguishably fused.

Origin.—The proximal third is attached narrowly by its lateral edge; the distal two thirds is attached broadly by its entire deep surface. The proximal third arises tendinously from the trochanteric ridge and the proximal end of the anterior intermuscular line and fleshily from a narrow area of the femur adjacent (medial) to the latter; the distal part arises tendinously from the anterior intermuscular line and fleshily from a broad adjacent area on the anteromedial surface of the femur, terminating distally at the level of the proximal end of the internal condyle; the posterior edge contacts the origin of M. femoritibialis internus.

Insertion.—Attachment is in common with M. vastus lateralis pars lateralis, which see.

Innervation.—Two or more branches of the middle division of the femoral nerve penetrate the anterior surface of the fused Mm. vastus medialis and vastus lateralis pars lateralis; a variable number of branches of the same division penetrate the medial surface of the proximal part of M. vastus medialis.

Individual Variation.—None of significance in any of the three species studied.

M. Femoritibialis Internus, Figs. 13, 15

T. pallidicinctus

General Description and Relations.—Elongate; on posteromedial surface of femur; bounded anteriorly by M. vastus medialis and posteriorly by M. adductor profundus (overlapping anterior edge of latter); anteroproximal part lateral to M. ambiens; anterodistal corner deep to distal end of M. extensor iliotibialis anticus; distal part of muscle split into superficial and deep layers; superficial layer thin, narrow, and tendinous except for proximal end; deep layer wider, much thicker, and fleshy except for distal end taking form of flat tendon; anterior edge of latter somewhat fused to medial edge of tendon of M. vastus medialis; deep layer widest near distal end of fleshy part; posterior edge of superficial layer fused to underlying deep layer, and anterior edge fused to (continuous with) posterior edge of tendon of M. extensor iliotibialis anticus.

Origin.—The origin is mostly fleshy from the posteromedial surface of the femur between the origin of M. vastus medialis and the posterior intermuscular line, terminating immediately proximal to the internal condyle.

INSERTION.—The tendons of both superficial and deep layers attach to the medial part of the rotular crest, forming the medialmost part of the patellar tendon.

INNERVATION.—The posteriormost branch of the middle division of the femoral nerve penetrates the medial surface of the muscle near the proximal end.

INDIVIDUAL VARIATION.—None of significance in any of the three species studied.

M. Extensor Iliofibularis (M. biceps femoris), Figs. 12, 14, 16, 17

The term extensor in the name of this muscle does not refer to its function. Howell (1938) used the term extensor to indicate derivation of the muscle from the primitive dorsal extensor muscle mass. (Likewise he used the term flexor to indicate derivation from the primitive ventral flexor muscle mass.)

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Deep to M. extensor iliotibialis lateralis and posterior to femur; broad proximally and narrow distally; posterior to M. vastus lateralis and anterior to proximal part of M. flexor cruris lateralis (superficial to distal part of latter); anteroproximal part aponeurotic, fused to deep surface of aponeurosis of M. extensor iliotibialis lateralis; proximal part of aponeurosis of M. extensor iliofibularis also fused to dorsal edges of underlying Mm. gluteus profundus and piriformis.

ORIGIN.—The posterior part is fleshy from the ventromedial surface of the entire lateral iliac process; the anterior part is aponeurotic from the posterior part of the anterior iliac crest.

INSERTION.—The tendon forms along the posterodistal edge of the belly and continues beyond the end of the belly as a cylindrical tendon that passes through the tendinous guide loop (the belly terminates approximately at the level of the guide loop), then extends anterodistally into the shank musculature; the tendon passes between the medial and lateral heads of M. flexor perforatus digiti IV, between the medial and lateral heads of M. flexor perforatus digiti II, lateral to the common tendon of the anterolateral heads of Mm. flexor perforatus digiti IV, flexor perforatus digiti II, and flexor perforatus digiti III, and between the posterior and lateral heads of M. flexor digitorum longus, attaching to the fibular tubercle.

The tendinous guide loop has three arms—proximal femoral, distal femoral, and fibular; the proximal and distal femoral arms unite posterior to the tendon of M. extensor iliofibularis; the proximal arm is medial to, and the distal arm is lateral to, the latter; the fibular arm joins the distal edge of the distal arm lateral to the tendon of M. extensor iliofibularis. The proximal arm extends anteroproximally lateral to the medial head of M. flexor perforatus digiti IV and medial to M. vastus lateralis pars postica, attaching to a narrow line on the anterolateral surface of the femur a short distance proximal to the external condyle and adjacent (posterior) to the origin of M. vastus lateralis pars postica. The distal arm extends anteriorly medial to the posterior head of M. flexor perforans et perforatus digiti II and medial to M. vastus lateralis pars postica, attaching in common with the tendon of origin of M. gastrocnemius pars externa to a small oval area on the posterolateral surface

of the femur a short distance proximal to the fibular groove; the arm is also fused to the underlying articular capsule. The fibular arm (broadest of the three) passes deep to, and fused with, the common tendon of origin of the lateral heads of Mm. flexor perforatus digiti IV and flexor perforatus digiti II, superficial to the common tendon of origin of the anterolateral heads of Mm. flexor perforatus digiti IV, flexor perforatus digiti II, and flexor perforatus digiti III, and deep to the tendon of M. ambiens, attaching broadly to a narrow line on the anterolateral surface of the proximal part of the fibula; the arm is also fused to the underlying articular capsule.

Innervation.—A branch of the middle peroneal division of the sciatic nerve sends twigs to the deep surface of the anteroproximal part; the dorsal peroneal division of the sciatic nerve penetrates the deep surface of the proximal end.

Individual Variation.—In some instances a variable number of twigs arises from the peroneal nerve near the middle of the thigh and enters the deep surface of the muscle. They are difficult to expose without breaking and may have been overlooked in some specimens.

T. cupido

Individual Variation.—The same variation is found as in *T. pallidicinctus* (see above). In one leg, the tendon of insertion bifurcates into proximal and distal arms before attaching.

P. p. jamesi

Differences from Typical *T. pallidicinctus*.—It arises from the ventral rather than the ventromedial surface of the lateral iliac process (there is no ventromedial surface to this process).

Individual Variation.—In nearly all of the legs, minute twigs to M. extensor iliofibularis come off the peroneal nerve near the middle of the thigh. The insertional tendon tends toward doubleness in two legs.

M. Piriformis (M. gluteus medius et minimus), Figs. 16, 20H, I

T. pallidicinctus

General Description and Relations.—Small, thin, and triangular; lateral to antitrochanter and posterior part of trochanter; deep to M. extensor iliofibularis and posterior (adjacent) to M. gluteus profundus; distal half (or more) tendinous.

Origin.—The muscle arises fleshily from the posterior end of the anterior iliac crest (ventral to the origins of Mm. extensor iliotibialis lateralis and extensor iliofibularis) beginning adjacent to the posterior end of M. gluteus profundus.

Insertion.—The flat tendon narrows, overlaps the anteroproximal corner of insertion of M. flexor ischiofemoralis, and attaches to the lateral surface of the proximal part of the femur immediately anterior to the insertion of M. flexor ischiofemoralis and posterior to the proximal end of M. vastus lateralis; the attachment is posterodistal to the insertion of M. iliotrochantericus medius and posteroproximal to the insertion of M. iliacus.

INNERVATION.—The small anterior peroneal division of the sciatic nerve turns anteriorly immediately after emerging from the ilio-ischiatic fenestra and passes deep to M. piriformis, giving twigs to the deep surface.

INDIVIDUAL VARIATION.—In both legs of one specimen, the insertion does not overlap the insertion of M. flexor ischiofemoralis. The posteroproximal corner of the muscle is tendinous in one leg.

T. cupido

INDIVIDUAL VARIATION.—The anterior border is somewhat fused with the posterior edge of M. gluteus profundus in one leg, while in another there is a slight gap between the origins of M. gluteus profundus and M. piriformis. In one leg, the posterior edge of the origin is aponeurotic. On both sides of one specimen, an accessory tendinous band arises several mm. posterior to the main part of M. piriformis and joins the proximal part of the insertional tendon, thus forming a Y-shaped unit (fig. 20I); the accessory tendon arises from the anterior end of the lateral iliac process (left side) or from the anterior part of the lateral iliac fossa (right side). The insertion may be proximal (rather than posterior) to the proximal end of M. vastus lateralis. In one leg, the insertional tendon is partly fused to the insertional tendon of M. flexor ischiofemoralis.

P. p. jamesi

INDIVIDUAL VARIATION.—There is often a gap between the origins of M. gluteus profundus and M. piriformis. In one leg (fig. 20H), the posteroproximal corner of the muscle is aponeurotic. The insertion is often proximal (rather than posterior) to the proximal end of M. vastus lateralis. In one instance, the insertion does not overlap the insertion of M. flexor ischiofemoralis.

M. Gluteus Profundus (M. iliotrochantericus posterior), Figs. 14, 16

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Large and thick; covering dorsolateral surface of entire preacetabular part of ilium; deep to Mm. extensor iliotibialis lateralis and extensor iliotibialis anticus; bounded posteriorly by M. piriformis and ventrally by M. iliacus; ventral edge fused with anterior part of latter and with proximal accessory aponeurosis of M. extensor iliotibialis lateralis; tough sheet of fascia strongly fused to anterior two thirds of lateral surface; posterior to this, fascia overlying muscle but not attaching to it; posterior half of fascia fused to overlying aponeurosis of M. extensor iliotibialis lateralis; deep surface of muscle somewhat fused to proximal part of M. iliotrochantericus medius.

ORIGIN.—The superficial surface is tendinous from the entire anterior iliac crest except the posterior end and from the crest forming the anterior and anterolateral edges of the ilium; the muscle arises fleshily from the entire dorsolateral surface of the preacetabular ilium as far posteriorly as the level of the pectineal process; the dorsal edge is adjacent (anterior) to the origin of M. piriformis.

INSERTION.—The attachment is by a short, wide, thick tendon to a curved line (convex anteriorly) on the lateral surface of the femoral trochanter.

INNERVATION.—The anterodorsal division of the femoral nerve turns dorsally

through the femoral notch of the ilium and penetrates the deep surface of the ventral part of the muscle midway of its length; the anterior peroneal division of the sciatic nerve passes deep to M. piriformis and terminates near the posterodorsal edge of M. gluteus profundus.

Individual Variation.—On both sides of one specimen, the branch from the femoral nerve passes lateral to the extreme anteroproximal corner of M. iliotrochantericus medius instead of through the femoral notch.

T. cupido

Individual Variation.—In one leg, the insertional tendon is strongly fused to the insertional tendon of M. iliotrochantericus medius.

P. p. jamesi

Individual Variation.—None of significance.

M. Iliacus (M. iliotrochantericus anterior), Figs. 13, 14, 15, 16, 17

T. pallidicinctus

General Description and Relations.—Adjacent ventrally to ventrolateral edge of M. gluteus profundus; lateral edge much thicker than medial edge; deep to M. extensor iliotibialis lateralis and anterolateral to M. iliotrochantericus medius; distal (posterior) end passing between proximal ends of Mm. vastus medialis and vastus lateralis pars lateralis; insertion overlapped by latter; dorsal surface of anterior part fused with ventrolateral edge of M. gluteus profundus and with ventral surface of proximal accessory aponeurosis of M. extensor iliotibialis lateralis; ventral surface partly fused with distal accessory aponeurosis of latter muscle.

Origin.—The origin is fleshy and tendinous from the lateral edge of the anterior part of the ilium.

Insertion.—The attachment is by a short flat tendon to the lateral surface of the femur distal to the trochanter and anterodistal to the insertion of M. piriformis and deep to the proximal part of M. vastus lateralis pars lateralis.

Innervation.—The dorsal division of the femoral nerve penetrates the ventral surface.

Individual Variation.—The dorsal division of the femoral nerve may fuse proximally with either the anterior or middle division. In one leg, there are two separate branches to the muscle.

T. cupido

Individual Variation.—The insertion may not be overlapped by M. vastus lateralis. The dorsal division of the femoral nerve is fused proximally with the middle division in one leg.

P. p. jamesi

Differences from Typical *T. pallidicinctus*.—The fleshy origin is wider.

Individual Variation.—The dorsal division of the femoral nerve may fuse proximally with either the anterior or middle division. In one leg, there are two branches to M. iliacus, one fused with the anterior division and the other with the middle division.

M. Iliotrochantericus Medius, Figs. 17, 20A, B, C, D

T. pallidicinctus

General Description and Relations.—Small and triangular; ventral to posterior half of M. gluteus profundus; all but posteroventral corner deep to latter; posteromedial to M. iliacus, anterior to neck of femur, and dorsolateral (adjacent proximally) to M. psoas; proximal end notched at level of femoral notch for passage of anterodorsal division of femoral nerve; part anterior to femoral notch mainly tendinous; dorsal surface of proximal part somewhat fused to M. gluteus profundus, proximal accessory aponeurosis of M. extensor iliotibialis lateralis split into two sheets enclosing and fusing with M. iliotrochantericus medius, ultimately attaching to lateral edge of ilium in common with origin of latter muscle.

Origin.—The muscle arises from the ventrolateral surface of the ilium anterior to the acetabulum and posterior to the origin of M. iliacus; the anterior part attaches to the ventrolateral edge of the ilium and the posterior part attaches just above the ventral edge. The muscle is not attached to the concavity of the femoral notch (the origin is notched here). The part attaching anterior to the femoral notch is narrow, tendinous, and continous anteriorly with the accessory aponeurosis of M. extensor iliotibialis lateralis (thus the anterior border of the muscle cannot be exactly delimited). The part attaching posterior to the femoral notch is wider and fleshy (fig. 20A).

Insertion.—The short flat tendon attaches to the lateral surface of the distal end of the trochanter slightly anterior and immediately distal to the insertion of M. gluteus profundus; the attachment is proximal to the origin of M. vastus lateralis, anteroproximal to the insertion of M. piriformis, and several mm. proximal to the insertion of M. iliacus.

Innervation.—The small posterodorsal division of the femoral nerve penetrates the ventral surface.

Individual Variation.—On both sides of one specimen, the femoral notch is absent and the proximal end of the muscle is not notched; the proximal part is entirely fleshy and the anterior border is well defined (fig. 20D).

T. cupido

Individual Variation.—The part attaching anterior to the femoral notch has a fleshy origin in one leg (fig. 20B), but in another, no part attaches anterior to the femoral notch (thus the muscle is not notched). In one leg, the insertional tendon is strongly fused to, and continuous with, the ventral edge of the insertional tendon of M. gluteus profundus.

P. p. jamesi

Individual Variation.—The part attaching anterior to the femoral notch may be mainly or entirely fleshy. In one leg, the part attaching anterior to the femoral notch is entirely separate from, although overlapped by, the main part of the muscle for the entire length of the fleshy belly (fig. 20C); both parts have a common insertional tendon.

M. Psoas (M. iliacus), Figs. 13, 15, 18

T. pallidicinctus

General Description and Relations.—Small and slender; on medial aspect of proximal end of thigh lateral to proximal end of M. ambiens; ventromedial to M. iliotrochantericus medius; proximal end visible from inside pelvis (medial to inguinal ligament); passes dorsolateral to inguinal ligament.

Origin.—The muscle arises fleshily from the ventrolateral edge of the ilium posterior to the femoral notch and ventral (adjacent) to the origin of M. iliotrochantericus medius.

Insertion.—The attachment is tendinous to the medial surface of the femur a short distance proximal to the origin of M. femoritibialis internus.

Innervation.—The posterior division of the femoral nerve, which spirals completely around M. psoas, gives several twigs into the proximal part.

Individual Variation.—None of significance.

T. cupido

Individual Variation.—In two legs the insertion is partly fleshy.

P. p. jamesi

Individual Variation.—In one leg the insertion is partly fleshy. The posterior division of the femoral nerve perforates the muscle in one instance.

M. Flexor Cruris Lateralis (M. semitendinosus), Figs. 12, 13, 14, 15, 16, 17

This muscle represents only the main head of the muscle for which Fisher and Goodman (1955) used the same name. Their accessory head of M. flexor cruris lateralis is here termed M. femorocruralis.

T. pallidicinctus

General Description and Relations.—Large, thick, and strap-shaped; on posterior surface of thigh; proximal part bounded anteriorly by Mm. extensor iliotibialis lateralis and extensor iliofibularis; anterodistal part deep to latter; bounded medially by Mm. caudofemoralis (proximally) and flexor cruris medialis (distally); proximal end much narrower than remainder and posterior to ilium; fused to underlying tough membrane, which forms body wall posterior to ilium; proximal half of narrow part aponeurotic; distal part of muscle posterior to M. femorocruralis; separated from latter by common raphe to which both attach; caudal muscle (M. transversoanalis) attached aponeurotically to superficial surface of posteroproximal fleshy part of M. flexor cruris lateralis.

Origin.—The origin is tendinous (superficial surface) and fleshy from the entire dorsolateral iliac ridge and fleshy from an area of the ilium below this ridge, also tendinous from the posterior edge of the ilium medial to the dorsolateral iliac ridge, and also tendinous from the transverse processes of the first free caudal vertebra and the vertebra either anterior or posterior to the latter.

Insertion.—M. flexor cruris lateralis and M. femorocruralis insert broadly on opposite sides of a long tendinous raphe that extends parallel to, but some distance posterior to, the distal half of the femur; the distal end of this tendon

broadens somewhat and fuses to the medial surface of M. gastrocnemius pars media (continuous with the tendon of the latter); the superficial part of this tendon continues toward the tibiotarsus, soon fusing to the deep surface of the overlying tendon of M. flexor cruris medialis; thus the common tendon of M. flexor cruris lateralis and M. femorocruralis insert in common with both M. flexor cruris medialis and M. gastrocnemius pars media.

Innervation.—A branch of the middle tibial division of the sciatic nerve enters the substance of M. caudofemoralis pars iliofemoralis, and emerges near its ventral edge, then passes lateral to M. caudofemoralis pars caudifemoralis and enters the anterior part of M. flexor cruris lateralis.

Individual Variation.—In three legs, the nerve does not perforate M. caudofemoralis pars iliofemoralis, but passes deep to it.

T. cupido

Individual Variation.—In one leg, a small accessory slip arises from the ventrolateral surface of the caudal musculature and joins the posterior edge of the main part of M. flexor cruris lateralis a short distance dorsal to the pubis. In several legs, the nerve does not perforate M. caudofemoralis pars iliofemoralis, but passes deep to it.

P. p. jamesi

Differences from Typical *T. pallidicinctus*.—The muscle is wider. The extreme proximal end is fleshy up to its origin, which is fleshy and tendinous from the vertebrae. The common insertional tendon of M. flexor cruris lateralis and M. femorocruralis fuses with the distal end of the fleshy part (instead of tendon) of M. flexor cruris medialis.

Individual Variation.—None of significance.

M. Flexor Cruris Medialis (M. semimembranosus), Figs. 12, 13, 14, 15, 16, 17, 20E

T. pallidicinctus

General Description and Relations.—Most posterior muscle on medial surface of thigh; long and strap-shaped; bounded anteriorly by M. adductor profundus; posteroproximal corner of latter medial to anteroproximal part of M. flexor cruris medialis; bounded laterally by Mm. caudofemoralis (proximally) and flexor cruris lateralis (distally); anteroproximal corner adjacent to posteroventral corner of M. flexor ischiofemoralis and lateral to extreme posteroproximal corner of M. adductor superficialis; distal end tendinous, extending into proximal part of shank; bounded medially by M. gastrocnemius pars interna and laterally by Mm. gastrocnemius pars media and plantaris.

Origin.—The muscle arises by a wide flat tendon from a narrow line on the lateral surface of the ischium dorsal to the ventral ischiatic tubercle.

Insertion.—The wide flat tendon attaches to a narrow line on the medial surface of the proximal part of the tibiotarsus a short distance anterior to the proximal part of M. plantaris and deep to M. gastrocnemius pars interna; the proximal end attaches immediately anterior to the distal end of the medial collateral ligament. Part of the common tendon of Mm. flexor cruris lateralis and femorocruralis fuses with the lateral surface of the tendon of M. flexor cruris medialis, inserting in common with it.

Innervation.—A branch of the middle tibial division of the sciatic nerve passes deep to both heads of M. caudofemoralis and enters the anterior part of M. flexor cruris medialis.

Individual Variation.—In several legs, the anterior edge of the proximal part fits into a deep longitudinal groove in the posterior edge of the proximal part of M. adductor superficialis; the two muscles fuse slightly at this point.

T. cupido

Individual Variation.—In two legs, the extreme posterior end of the origin is from the pubis. In two others, the proximal end is separated by a slight gap from M. adductor superficialis. The nerve arises from the posterior (rather than middle) tibial division in one leg.

P. p. jamesi

Differences from Typical *T. pallidicinctus*.—The origin is wider; the posterior third to half of the origin is fleshy. The entire origin is from a strongly curved line, the middle part of which attaches to the ventral edge of the ischium posterior to the ventral ischiatic tubercle. The insertion is wider. The insertional tendon attaches posterior (rather than anterior) to the distal end of the medial collateral ligament; the proximal end of the insertion attaches to the articular capsule (fig. 20E). The insertional tendon is shorter; as a result, the common tendon of Mm. flexor cruris lateralis and femorocruralis fuses with the distal end of the fleshy belly (instead of the tendon) of M. flexor cruris medialis.

Individual Variation.—In two thirds of the legs, the proximal part of the insertion is fleshy rather than tendinous. In one leg, the middle part of the insertional tendon spilts into two sheets, one attaching anterior to and one attaching posterior to the distal end of the medial collateral ligament. The nerve may arise from the posterior tibial division (two legs), from the middle tibial division (one leg), or as an independent division of the tibial nerve (three legs). In one leg, the nerve perforates the lateral part of M. flexor ischiofemoralis.

M. Caudofemoralis (M. piriformis), Figs. 12, 13, 14, 15, 16, 20J

T. pallidicinctus

General Description and Relations.—Posterior to proximal part of shaft of femur and deep to M. extensor iliofibularis; posterior part deep to M. flexor cruris lateralis; bounded medially by Mm. flexor ischiofemoralis (dorsally), flexor cruris medialis (posteriorly), and adductor superficialis (anteroventrally); anterior end distal to anterior end of M. flexor ischiofemoralis; two distinct heads—pars iliofemoralis and pars caudifemoralis; *pars iliofemoralis* dorsal to pars caudifemoralis; posteroventral corner of former overlapped by latter; pars iliofemoralis wider and much shorter than pars caudifemoralis; extreme posterior end of pars iliofemoralis fused to overlying posteroproximal aponeurosis of M. extensor iliotibialis lateralis; small part of ventral edge sometimes fused with underlying tendinous posteroproximal corner of M. flexor cruris medialis; entirely fleshy except for small triangular tendinous area along dorsal margin at point where branch of middle tibial division of sciatic nerve passes deep to muscle; *pars caudifemoralis* long, thin,

narrow, and strap-shaped; overlapping posteroventral corner of ischium; posterior end of fleshy belly narrowed and forming long slender tendon passing into caudal musculature; anterior end forming short narrow tendon fused to deep surface of ventral edge of pars iliofemoralis relatively near insertion; tendon continuous to insertion; fleshy anterodorsal corner of pars caudifemoralis slightly overlapped by ventral edge of pars iliofemoralis; some form of connection usually present between anterior part of M. caudofemoralis pars caudifemoralis and dorsal end of raphe between Mm. flexor cruris lateralis and femorocruralis, most often consisting of narrow weak tendon.

ORIGIN.—*Pars iliofemoralis:* This arises fleshily from the ventromedial surface of the posterior part of the lateral iliac process, from the entire lateral ischiatic ridge, and from the lateral surface of the ischium anterior to this ridge nearly as far forward as the posterior edge of origin of M. flexor ischiofemoralis; the posteroventral corner reaches the ventral edge of the ischium and usually attaches to the ischiopubic membrane posterior to M. flexor cruris medialis. *Pars caudifemoralis:* This arises by a narrow tendon from the ventral surface of a broad, thick, tendinous sheet ventral to the pygostyle, which, in turn, attaches to the ventral surface of the pygostyle.

INSERTION.—The common belly formed by the union of the two heads narrows (width variable) and attaches to the posterolateral surface of the femur distal to the level of insertion of M. iliacus and in contact with the posterior edge of origin of M. vastus lateralis pars lateralis; the dorsal part is fleshy and the ventral part is tendinous.

INNERVATION.—A branch of the middle tibial division of the sciatic nerve gives several twigs to the deep surface of pars iliofemoralis; another twig enters the substance of pars iliofemoralis and emerges from the ventral edge of the latter, then enters the dorsal edge of pars caudifemoralis. The latter twig was not found in all legs, but was probably destroyed during dissection.

INDIVIDUAL VARIATION.—The tendinous area in the dorsal margin of pars iliofemoralis is lacking in one leg and extremely small in some others. In both legs of one specimen, the connection between M. caudofemoralis pars caudifemoralis and the raphe between Mm. flexor cruris lateralis and femorocruralis consists of a small (11×2 mm.) but well developed and entirely fleshy muscle slip (fig. 16). In one leg, the ventral third of this connection is fleshy, the remainder tendinous; in another, this connection is completely lacking.

T. cupido

INDIVIDUAL VARIATION.—The tendinous area in the dorsal margin of pars iliofemoralis is lacking in one leg. The connection between pars caudifemoralis and the raphe between Mm. flexor cruris lateralis and femorocruralis is lacking in several legs. A conspicuous variation occurring in three legs is the presence of a tendinous area in the belly of pars caudifemoralis, dividing the latter into proximal and distal parts (fig. 20J). In one leg, the posteroventral corner of pars iliofemoralis arises from the pubis. The origin of pars caudifemoralis in three legs is directly from the anteroventral surface of the pygostyle. In one instance, the insertional tendon of pars caudifemoralis is long and extremely slender and extends for some distance in a groove on the medial surface of pars iliofemoralis before fusing with the latter.

P. p. jamesi

Differences from Typical *T. pallidicinctus*.—There is no connection at all between pars caudifemoralis and the raphe between Mm. flexor cruris lateralis and femorocruralis. The posteroventral corner of pars iliofemoralis is some distance dorsal to the ventral edge of the ischium and, therefore, does not attach to the ischiopubic membrane.

Individual Variation.—The insertion (narrow) is entirely tendinous in one leg.

M. Flexor Ischiofemoralis (M. ischiofemoralis), Figs. 16, 17

T. pallidicinctus

General Description and Relations.—Thick; on lateral surface of anterior part of ischium; posterior end in lateral iliac fossa; deep to Mm. extensor iliofibularis and caudofemoralis pars iliofemoralis; overlapping ventral extrapelvic part of M. obturator and anteroproximal part of M. adductor superficialis (slightly fused to proximal edge of latter); posteroventral corner contacting anteroproximal corner of M. flexor cruris medialis; extreme anterodorsal corner usually overlapped by tendon of M. piriformis.

Origin.—The muscle arises fleshily from a large area on the lateral surface of the ischium extending ventrally to the origin of M. adductor superficialis, anteriorly to the level of the posterior end of the obturator foramen, dorsally to the ventral border of the ilio-ischiatic fenestra and to the depth of the lateral iliac fossa, and posteriorly approximately to the level of the ventral ischiatic tubercle.

Insertion.—The short flat tendon attaches to the lateral surface of the femur immediately posterior to the insertion of M. piriformis.

Innervation.—The posterior tibial division of the sciatic nerve penetrates the dorsal surface.

Individual Variation.—The ventral part of the insertion may be fleshy.

T. cupido

Individual Variation.—None of significance.

P. p. jamesi

Individual Variation.—In all the legs except one, an additional twig arises from the branch to M. flexor cruris medialis and penetrates the lateral surface of M. flexor ischiofemoralis. The ventral part of the insertion is fleshy in one leg.

M. Adductor Superficialis (M. adductor longus et brevis, pars externa), Figs. 14, 16, 17

T. pallidicinctus

General Description and Relations.—Posterior to femur, lateral to M. adductor profundus, and medial to Mm. flexor ischiofemoralis, caudofemoralis, and femorocruralis; proximal end (fleshy) fused to proximal tendinous end of M. adductor profundus.

Origin.—The origin is fleshy and tendinous from the proximal end of the lateral surface of M. adductor profundus and from a narrow line on the ischium

adjacent (dorsal) to the origin of the latter; the posterior part of the origin sometimes extends farther dorsally on the lateral surface of the ischium; the origin does not extend so far anteriorly nor so far posteriorly as the origin of M. adductor profundus; the anterior edge is at the posterior border of the obturator foramen.

INSERTION.—The attachment is fleshy and thick (distal end thin) to the posterior surface of the middle part of the femur between the posterior and posterolateral intermuscular lines; the attachment is adjacent (lateral) to the insertion of M. adductor profundus and adjacent (medial) to the origins of Mm. vastus lateralis (proximally) and femorocruralis (distally); the proximal edge is approximately at the level of the distal edge of the insertion of M. caudofemoralis.

INNERVATION.—A branch of the obturator nerve emerges from the obturator foramen dorsal to the tendon of insertion of M. obturator pars postica, turns ventrally (crossing latter), and passes deep to the anteroproximal corner of M. adductor superficialis, extending posterodistally between the adductor muscles and giving twigs to the medial surface of M. adductor superficialis and to the lateral surface of M. adductor profundus.

INDIVIDUAL VARIATION.—The anterior edges of the two adductor muscles are so firmly fused together in some cases that the boundaries cannot be identified at this point. In several legs, there is a deep longitudinal groove in the posterior edge of the proximal part of the muscle into which the anterior edge of M. flexor cruris medialis fits.

T. cupido

INDIVIDUAL VARIATION.—In some cases, the anterior edges of the two adductor muscles are firmly fused together.

P. p. jamesi

DIFFERENCES FROM TYPICAL *T. pallidicinctus*.—The origin is narrower.

INDIVIDUAL VARIATION.—The anterior edges of the two adductor muscles may be fused together. In one leg, the entire muscle is indistinguishably fused with M. adductor profundus and they appear as a single muscle.

M. Adductor Profundus (M. adductor longus et brevis, pars interna), Figs. 13, 15, 17, 18

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Broad; on medial surface of thigh immediately posterior to femur; bounded posteriorly by M. flexor cruris medialis (medial to anteroproximal corner of latter), anteriorly by M. femoritibialis internus (anterior edge overlapped by latter), and laterally by Mm. adductor superficialis and femorocruralis; proximal end tendinous (except anterior edge), fused to proximal fleshy end of M. adductor superficialis.

ORIGIN.—The muscle arises tendinously from the ventral edge of the ischium extending from the posterior border of the obturator foramen to the ventral ischiatic tubercle and (anterior edge) fleshily from the lateral surface of the pubis ventral to the obturator foramen; the origin is adjacent (ventral) to the origin of M. adductor superficialis.

Insertion.—The attachment is fleshy and tendinous from the posterior intermuscular line and (proximally and distally) from a narrow adjacent area. Proximally there are often two approximately parallel lines a short distance apart, representing points of attachment of the lateral and medial edges of the muscle; if there is only one line proximally, it may represent the attachment of either the lateral or medial edge of the muscle; distally there is usually only one line, representing the lateral edge of the muscle. The distal end extends onto the posterior surface of the proximal part of the internal condyle, and is adjacent (lateral) to the origin of M. femoritibialis internus, adjacent (medial) to Mm. adductor superficialis and femorocruralis, and adjacent (proximal) to M. gastrocnemius pars media.

Innervation.—See M. adductor superficialis.

Individual Variation.—The anterior edges of the two adductor muscles are strongly fused together in some cases.

T. cupido

Individual Variation.—The anterior edge may be fused with that of M. adductor superficialis. The distal end is sometimes slightly fused with M. gastrocnemius pars media. In one leg, the proximal two thirds of the insertion is entirely tendinous, whereas in another the distal end of the insertion is tendinous.

P. p. jamesi

Individual Variation.—The anterior edge (in one leg the entire muscle) in some legs fuses with that of M. adductor superficialis.

M. Obturator (M. obturator externus + M. obturator internus), Figs. 16, 17, 18, 19C, D, 20K, L, M

I am adopting the single name M. obturator for the complex that Fisher (Fisher, 1946; Fisher and Goodman, 1955) subdivides into Mm. obturator externus and obturator internus. The reasons for this change are given in the section on terminology.

For ease of description, it is desirable to apply names to the subdivisions of M. obturator. It has been customary to divide the obturator complex into two parts—an obturator internus and an obturator externus; the latter has often been further subdivided. The evidence given below demonstrates that a primary division of the complex into only two parts is unsatisfactory.

I strongly suspect that comparable parts of the obturator complex have been considered a part of the "internus" in some birds and a part of the "externus" in others. In their work on the Galliformes, Hudson, *et al.* (1959) subdivide the obturator complex into only two divisions—obturator externus and obturator internus. The extrapelvic part of this complex that arises from the rim of the obturator foramen and inserts in common with the stout tendon of the main intrapelvic part of the obturator internus is considered by them to be a part of the obturator internus. Their obturator externus lies anterior and deep to the extrapelvic part of the obturator internus and inserts separately from the latter. (I also have found this same arrangement in *Tympanuchus* and *Pedioecetes*.)

Berger (1952), in his description of the Black-billed Cuckoo (*Coccyzus erythrophthalmus*), also divides the obturator complex into an obturator in-

ternus and an obturator externus; the latter he subdivides into a dorsal and a ventral part. He states (p. 530) that he did not find any measurable differences in myology between *C. erythrophthalmus* and *C. americanus.* In order better to compare this arrangement with that in *Tympanuchus,* I have examined two specimens of *C. americanus.* My findings in the latter differ from Berger's description (p. 541) in one respect. Whereas Berger states that the dorsal and ventral parts of M. obturator externus are distinct except at their origin, I find them fused for their entire length; the muscle fibers that connect these two parts lie deep to the tendon of M. obturator internus. The origin of all parts of the complex in *Coccyzus* is similar to that in *Tympanuchus.* The only notable difference in configuration is that the part in *Coccyzus* that appears to correspond to the obturator externus of Hudson, *et al.* (1959) is not separate from the remainder of the extrapelvic part of the muscle. Berger (1952) considers all parts of the muscle having an extrapelvic origin to make up the obturator externus. It appears to me that the dorsal part and a part of the ventral part of the obturator externus of Berger correspond to the extrapelvic fleshy part of the obturator internus of Hudson, *et al.*

From my limited study, it seems to me to be desirable to recognize four subdivisions of the obturator complex, for which I propose the terms pars antica, pars dorsalis, pars ventralis, and pars postica. These parts exhibit various degrees of fusion in different groups of birds and some parts appear to be absent in certain birds. A study of a wide variety of birds will be required to determine whether or not a subdivision into the four parts proposed here is suitable for birds as a whole.

Applying these terms to *Coccyzus,* pars postica is equivalent to the entire obturator internus of Berger (1952). Pars dorsalis is apparently equivalent to the dorsal part of Berger's obturator externus. The ventral part of the obturator externus of Berger represents the fused pars antica and pars ventralis.

The main parts of the obturator muscle appear to be pars postica and pars antica. Pars dorsalis and pars ventralis are more variable; in *Coccyzus* these two parts are closely associated with pars antica whereas in *Tympanuchus* they are most closely associated with pars postica. Apparently pars dorsalis and pars ventralis may be absent in some birds.

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Deeply situated immediately posterior to head of femur; part extending through obturator foramen and lying inside pelvis; extrapelvic part deep to Mm. flexor ischiofemoralis and piriformis; muscle partially divisible into four parts—pars antica, pars dorsalis, pars ventralis, and pars postica (fig. 20K); *pars postica:* mostly inside pelvis; much larger than other parts; broad (narrow anteriorly); on medial surface of ischium; composed of several fascicles; anterior end forming narrow, heavy tendon (with some fleshy fibers on posterior part of deep surface) passing through obturator foramen; anteriormost fleshy fibers of ventralmost fascicle fused with pars ventralis; *pars ventralis:* essentially extrapelvic (see origin); mostly ventral to tendon of pars postica; superficial to pars antica; fused to anterior fleshy part of pars postica; anterodorsal edge usually adjacent to, and often slightly fused with, ventral edge of pars dorsalis (deep to tendon of pars postica); *pars dorsalis:* entirely extrapelvic; mostly dorsal to tendon of pars

postica; superficial to dorsal part of pars antica; *pars antica:* extremely short but relatively thick; entirely fleshy; entirely extrapelvic; between obturator foramen and head of femur; anterior surface adjacent to articular capsule; almost completely covered by other parts of muscle; proximal end of posterior surface often slightly fused with adjacent parts of pars ventralis and pars dorsalis.

ORIGIN.—*Pars postica:* This arises fleshily from the medial surface of the entire ischium except the posterior end, from the dorsomedial and medial surfaces of the anterior half of the pubis as far forward as the obturator foramen, from the internal ilio-ischiatic crest, from the medial surface of the ilium for a short distance posterior to this crest, and from the iliac recess; the posteroventral corner usually arises from the medial surface of the ischiopubic membrane. *Pars ventralis:* This arises fleshily from the dorsomedial edge of the ventral border of the obturator foramen (fig. 20M) and (narrowly) from the anterior border of the foramen; this part may or may not arise from the lateral surface of the anteroventral border of the foramen and is usually adjacent along the anterior border of the foramen to pars dorsalis; pars ventralis is continuous along the ventral border of the foramen with the intrapelvic origin of pars postica. *Pars dorsalis:* This arises fleshily from the lateral surface of the anterodorsal border of the foramen (fig. 20L) and may extend posteriorly along the dorsal border of the foramen. *Pars antica:* This arises fleshily from the depresssed area anterior to the obturator foramen (adjacent to pars dorsalis and pars ventralis); the posteroventral corner may arise from the lateral surface of the anteroventral border of the obturator foramen (ventral to the anterior end of pars ventralis; fig. 20L).

INSERTION.—*Pars postica:* Several tendinous bands (intrapelvic) converge and coalesce, forming a single strong tendon that passes through the obturator foramen and attaches to the lateral surface of the femoral trochanter a short distance posterior to the insertion of M. gluteus profundus and proximal to the insertion of M. flexor ischiofemoralis. *Pars ventralis:* The attachment is fleshy and tendinous to the ventral edge and the deep surface of the tendon of pars postica. *Pars dorsalis:* The attachment is fleshy and tendinous to the dorsal edge of the tendon of pars postica. *Pars antica:* The attachment is fleshy to the posterior surface of the proximal end of the femur several mm. posterior to the insertion of pars postica; the lateral edge attaches to the obturator ridge.

INNERVATION.—The muscle is supplied by the obturator nerve; several twigs, which do not pass through the obturator foramen, penetrate the anterior part of the medial surface of pars postica; several twigs pass through the obturator foramen and supply pars dorsalis, pars ventralis, and pars antica.

INDIVIDUAL VARIATION.—In some cases the origin of pars postica does not include the dorsal end of the internal ilio-ischiatic crest nor the ilium posterior to it. Tiny but distinct accessory slips are sometimes present. In one leg a tendinous slip of parts antica extends beyond the remainder of the muscle and inserts independently on the trochanter close to the insertion of pars postica. In another leg, a fleshy and tendinous slip of pars antica attaches to the deep surface of the insertional tendon of pars postica. In still another leg, a fleshy and tendinous slip of pars dorsalis inserts adjacent (anterior) to the dorsal edge of the insertion of pars antica.

T. cupido

INDIVIDUAL VARIATION.—The variations are similar to those given above for *T. pallidicinctus* except that there is no slip of pars antica attaching to the tendon of pars postica.

P. p jamesi.

INDIVIDUAL VARIATION.—There are variations similar to those given above for *T. pallidicinctus* except that there is no independent slip of pars antica attaching on the trochanter close to the insertion of pars postica. Pars dorsalis may be quite small. In several legs, pars dorsalis is more closely associated with pars antica than with pars postica; in one of these, pars dorsalis is indistinguishably fused with pars antica (inserting with the latter) except for a few fibers which insert with pars postica.

M. Femorocruralis (M. accessorius semitendinosi), Figs. 14, 15, 16, 17

Fisher (Fisher, 1946; Fisher and Goodman, 1955) considers this muscle as an accessory head of M. flexor cruris lateralis. The reasons for this change in terminology are given in the section on terminology.

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Short and broad; posterior to distal part of femur; deep to Mm. extensor iliofibularis and vastus lateralis pars postica; bounded posteriorly by M. flexor cruris lateralis, medially by Mm. adductor superficialis and adductor profundus, and distally by M. gastrocnemius pars media; fused to a variable degree with the latter (in some cases these two muscles fused firmly together, appearing as single muscle); distal and medial to proximal end of M. flexor perforatus digiti IV.

ORIGIN.—The muscle arises fleshily (thin proximally, thick distally) from the posterior surface of approximately the distal half of the femur between the posterior and posterolateral intermuscular lines. The ventral end is continuous with the origin of M. gastrocnemius pars media, adjacent (medial) to the origin of M. vastus lateralis pars postica, and adjacent (lateral) to the insertions of Mm. adductor superficialis and adductor profundus.

INSERTION.—The attachment is to the tendinous raphe in common with M. flexor cruris lateralis (which see).

INNERVATION.—One or two tiny branches come off the tibial nerve near the distal end of the main trunk of the sciatic nerve, pass anteriorly deep to the peroneal nerve, and penetrate the lateral surface.

INDIVIDUAL VARIATION.—In two legs, the branch of the medial division of the tibial nerve which supplies M. gastrocnemius pars media sends a twig to the lateral surface of the distal end of M. femorocruralis (in addition to the usual innervation).

T. cupido

INDIVIDUAL VARIATION.—None of significance.

P. p. jamesi

Differences from Typical *T. pallidicinctus.*—The muscle is much wider, extending farther proximally on the femur.

Individual Variation.—None of significance.

M. Gastrocnemius, Figs. 12, 13, 15

T. pallidicinctus

General Description and Relations.—Divided into three distinct, widely separated parts—pars externa, pars interna, and pars media; *pars externa:* large; on posterolateral surface of shank; narrow proximally and distally; bounded anterolaterally by M. flexor perforans et perforatus digiti II and anteromedially by medial head of M. flexor perforatus digiti III; completely separate from pars interna and media except for common tendon of insertion; *pars interna:* large; on anteromedial surface of shank; narrow distally; bounded anterolaterally by M. peroneus longus and posteromedially by pars media (proximally) and medial head of M. flexor perforatus digiti III; broad sheet of tough connective tissue extending between distal parts of pars externa and pars interna; covering underlying M. flexor perforatus digiti III (medial head), somewhat fused with anteroproximal edge of M. peroneus longus; *pars media:* small and short; on medial surface of proximal part of shank; deep to tendon of insertion of M. flexor cruris medialis; bounded anteromedially by pars interna, posterolaterally by medial head of M. flexor perforatus digiti III, and proximally by M. femorocruralis; fused to latter, and boundary between the two difficult to locate.

Origin.—*Pars externa:* The short cylindrical tendon fuses with the anterior half of the distal arm of the tendinous guide loop for M. extensor iliofibularis and attaches in common with the latter to the posterolateral surface of the femur immediately proximal to the fibular condyle; the attachment is proximal (adjacent) to the origin of M. flexor perforans et perforatus digiti II and distal (adjacent) to the origin of M. flexor perforatus digiti IV and is fused to the articular capsule.

Pars interna: The proximal end is partly separable into two layers—a superficial longer one and a deep shorter one. The superficial layer attaches fleshily to the ventral part of the anterior surface of the patella and to the medial half of the superficial surface of the patellar tendon; this layer slightly overlaps the distal fleshy end of M. extensor iliotibialis anticus. The deep layer (overlapped by the superficial layer) attaches to the medial surface of the inner cnemial crest, to the rotular crest medial to the latter, to the medial surface of the proximal part of the tibiotarsus, and (posteroproximal corner) to the distomedial edge of the patellar tendon and to the articular capsule posteromedial to the rotular crest; the entire ventral edge is tendinous, the remainder fleshy.

Pars media: This arises fleshily from an oblique line beginning at the distal end of the origin of M. femorocruralis (continuous with the latter) and extending distomedially across the proximal part of the popliteal area to the proximal edge of the internal condyle, then attaching to the adjacent part of the articular capsule; this part is adjacent (distal) to the insertion of M. adductor profundus and adjacent (proximomedial) to the medial head of M. flexor perforatus digiti IV.

INSERTION.—*Pars media* narrows distally with a narrow tendon along the posterior edge of the fleshy belly; approximately one third of the way down the tibiotarsus the fleshy part terminates and the tendon joins the posterior edge of pars interna, continuing distally in this position. The ossified tendon on the superficial surface of the distal part of *pars interna,* continuous posteriorly with the tendon of pars media, is joined approximately two thirds of the way down the tibiotarsus by the tendon of pars externa; the fleshy belly of pars interna ends just below the junction. The ossified tendon on the superficial surface of the distal part of *pars externa* extends beyond the fleshy belly and becomes flexible before joining the tendon of pars interna and media. The common tendon (partly ossified) extends along the posterior surface of the tibiotarsus and widens as it passes posterior to the tibial cartilage, bound to the latter by a thin tough sheet of connective tissue which attaches to the edges of the tibial cartilage, thus forming a sheath for the tendon; the tendon attaches by its edges to the posterior edges of the calcaneal ridges of the hypotarsus, then continues distally (much reduced in thickness) along the posterior surface of the tarsometatarsus, enclosing the flexor tendons; the lateral edge of the tendon attaches to the posterolateral edge of the tarsometatarsus, terminating immediately above the level of the hallux; the medial edge attaches to the edge of the posterior metatarsal crest; the tendon terminates as a thin sheet that attaches to the fascia on the sole of the foot. (Hudson, *et al.*, 1959 consider the posterior metatarsal crest to be an ossified part of the tendon of M. gastrocnemius.)

INNERVATION.—A branch of the lateral division of the tibial nerve penetrates the proximal part of the medial surface of pars externa. One or two branches of the medial division of the tibial nerve pass deep to M. plantaris and penetrate the deep surface of the posterior part of pars interna. The most proximal branch of the medial division of the tibial nerve penetrates the lateral surface of pars media.

INDIVIDUAL VARIATION.—None of significance.

T. cupido

INDIVIDUAL VARIATION.—In one leg, the lateral edge of pars interna overlaps the proximomedial edge of M. peroneus longus; some fibers attach to the lateral surface of the inner cnemial crest.

P. p. jamesi

DIFFERENCES FROM TYPICAL T. *pallidicinctus*.—The proximal end of pars interna does not reach the patella.

INDIVIDUAL VARIATION.—In one leg, an additional twig to pars media arises from the distal branch to M. femorocruralis.

M. Flexor Perforans et Perforatus Digiti II, Figs. 12, 14

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Long, slender, and Y-shaped; on lateral surface of shank; the two heads enclosing M. flexor perforans et perforatus digiti III; *posterior head* bounded posteriorly by M. gastrocnemius pars externa; extreme proximal end deep to M. vastus lateralis pars postica; anterior surface fused to posterior surface of M. flexor perforans et perforatus digiti

III; deep surface fused to tendinous part of lateral head of M. flexor perforatus digiti IV; *anterior head* tendinous except for extreme distal end; covered by, and fused to, posterior edge of M. peroneus longus; fused to anterior surface of M. flexor perforans et perforatus digiti III; two heads join above middle of shank; anteroproximal and posterodistal parts of common belly usually tendinous.

ORIGIN.—*Anterior head:* This arises by a narrow tendon (partly ossified) from the distal tip of the outer cnemial crest. The tendon is so intimately fused with a connective tissue sheet fused to the deep and posterior surfaces of M. peroneus longus and to the anterior surface of M. flexor perforans et perforatus digiti III that M. flexor perforans et perforatus digiti II could be considered to arise from these two muscles. *Posterior head:* This arises mostly fleshily from the lateral surface of a compound sheet of tough connective tissue formed by the fusion of the tendinous posteroproximal corner of M. flexor perforans et perforatus digiti III, the proximal parts of the tendons of origin of the lateral heads of Mm. flexor perforatus digiti IV and flexor perforatus digiti II, the fibular and distal arms of the guide loop for M. extensor iliofibularis, and the lateral part of the articular capsule; a part of the common tendon of origin of the anterolateral heads of Mm. flexor perforatus digiti III, flexor perforatus digiti IV, and flexor perforatus digiti II also contributes to this sheet, which attaches to the lateral surface of the external condyle of the femur and to the anterolateral surface of the head of the fibula; for convenience in description, this complex connective tissue sheet will hereafter be termed the *femorofibular fascia.* The anteroproximal corner of the posterior head of M. flexor perforans et perforatus digiti II often attaches to the lateral surface of the vinculum that passes from the femorofibular fascia to the deep surface of the patellar tendon; the extreme proximal end usually attaches fleshily to a small area on the femur immediately proximal to the fibular condyle and adjacent (distal) to the attachment of the distal arm of the guide loop for M. extensor iliofibularis.

INSERTION.—The common belly terminates approximately two thirds of the way down the shank; the slender ossified tendon begins along the posteromedial edge of the common belly, continues distally along the posterior surface of the shank, and becomes flexible before passing through the canal in the tibial cartilage that lies posteromedial to the canal for M. flexor digitorum longus. The tendon passes with the tendon of M. flexor perforatus digiti II (medial to the latter) through a canal in the hypotarsus (see M. flexor perforatus digiti II); just below the hypotarsus, the tendon becomes superficial to the tendon of M. flexor perforatus digiti II and farther distally becomes lateral and finally deep to the latter; the tendon is ossified for most of the length of the tarsometatarsus. At the distal end of this bone, the tendon expands before passing onto the ventral surface of digit II between the tendons of Mm. flexor perforatus digiti II and flexor digitorum longus; at the level of the first phalanx, the edges of the tendon extend dorsally around the tendon of M. flexor digitorum longus and fuse, forming a sheath around the latter; the latter emerges from the sheath near the distal end of the first phalanx; the tendon attaches to the proximal end of the subarticular cartilage ventral to the first interphalangeal joint (the strongest attachment is on the medial side).

INNERVATION.—The lateral division of the tibial nerve sends twigs into the posteromedial edge of the posterior head.

INDIVIDUAL VARIATION.—In one leg, the fleshy part of the anterior head is unusually long. In another leg, the anterior head is entirely tendinous. In one leg, a bundle of fibers of the posterior head attaches to the deep surface of the distal part of the patellar tendon. In one leg, near the middle of the tarsometatarsus a rather long and narrow but thick and strong vinculum arises from the tendon of M. flexor perforatus digiti II and, farther distally, joins the tendon of M. flexor perforans et perforatus digiti II.

T. cupido

INDIVIDUAL VARIATION.—In one leg, the posterior head arises in part from the distolateral edge of the patellar tendon and in another, in part from the superficial surface of the distolateral corner of the patellar tendon.

P. p. jamesi

INDIVIDUAL VARIATION.—None of significance.

M. Flexor Perforans et Perforatus Digiti III, Figs. 12, 14

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Thick, bipinnate; on lateral surface of proximal part of shank between two heads of M. flexor perforans et perforatus digiti II; bounded anteriorly by M. peroneus longus; anterior surface fused with tendinous anterior head of M. flexor perforans et perforatus digiti II; anterolateral edge somewhat fused to posterior edge of M. peroneus longus superficial to latter tendon; posterior surface fused to posterior head of M. flexor perforans et perforatus digiti II; distal part of belly covered by common belly of latter muscle; posteromedial edge fused to underlying lateral head of M. flexor perforatus digiti IV; anteromedial edge usually somewhat fused to underlying M. flexor digitorum longus.

ORIGIN.—The origin is fleshy and tendinous from the edge of the outer cnemial crest and fleshy from the superficial surface of the distolateral part of the patellar tendon; the posteroproximal corner arises tendinously from the femorofibular fascia.

INSERTION.—The belly narrows abruptly, terminating approximately at the middle of the shank; the slender ossified tendon extends posterodistally along the shank, becoming flexible before passing posterior to the tibial cartilage deep to the tendon of M. gastrocnemius, medial to the tendon of M. flexor perforatus digiti IV, and superficial to the medial half of the tendon of M. flexor perforatus digiti III; a thin sheet of connective tissue covers the tendon and attaches by its edges to the underlying tendon of M. flexor perforatus digiti III (thus the latter tendon forms a sheath for the tendon of M. flexor perforans et perforatus digiti II); the tendon is ossified for most of the length of the tarsometatarsus; at midlength of the latter, the tendon lies between the tendons of Mm. flexor perforatus digiti IV and flexor perforatus digiti III; near the distal end of the tarsometatarsus, the tendon becomes lateral and then deep to the tendon of M. flexor perforatus digiti III and is connected by a vinculum to the latter (which see). The tendon enters the ventral surface of digit III between the tendons of Mm. flexor perforatus digiti III and flexor digitorum longus; after sending a dorsal slip (lateral to the tendon of M. flexor digitorum longus) to the subarticular cartilage ventral to the first

interphalangeal joint, the tendon divides into two branches, between which emerges the tendon of M. flexor digitorum longus; the lateral branch attaches to the subarticular cartilage of the second interphalangeal joint and to the lateral surface of the distal end of the second phalanx; the medial branch has similar attachments on the medial side of the digit.

Innervation.—A branch of the lateral division of the tibial nerve passes deep to the posterior head of M. flexor perforans et perforatus digiti II and enters the posteromedial edge of M. flexor perforans et perforatus digiti III.

Individual Variation.—In both legs of one specimen, the part arising from the femorofibular fascia appears as a distinct but short accessory head. There is no significant individual variation in *T. cupido* or *P. p. jamesi.*

M. Flexor Perforatus Digiti IV, Figs. 14, 16

T. pallidicinctus

General Description and Relations.—On posterolateral aspect of shank deep to M. gastrocnemius pars externa; bounded medially by medial head of M. flexor perforatus digiti III, anterolaterally by posterior head of M. flexor perforans et perforatus digiti II, and anteriorly by M. flexor digitorum longus; divided into three heads—medial (largest), lateral, and anterolateral (smallest); tendon of insertion of M. extensor iliofibularis passing between medial and lateral heads; proximal and anteroproximal parts of *lateral head* an extremely thin, flat tendon; anterodistal part of tendon fused to lateral surface of fleshy part of underlying lateral head of M. flexor perforatus digiti II; proximal part of tendon fused indistinguishably to tendinous part of underlying lateral head of M. flexor perforatus digiti II; fleshy part of *anterolateral head* anterodistal to lateral head; proximal part of former a long slender tendon anterior to lateral head; anterior surface of anterolateral head (both fleshy and tendinous parts) fused to tendon of anterolateral head of M. flexor perforatus digiti III; deep surface fused to underlying anterolateral head (fleshy) of M. flexor perforatus digiti II; common tendon of anterolateral heads of M. flexor perforatus digiti IV and M. flexor perforatus digiti III passing medial to tendon of insertion of M. extensor iliofibularis, to peroneal nerve, and to fibular arm of guide loop for M. extensor iliofibularis; tendon of M. ambiens inserting on anterolateral surface of this common tendon; *medial head* entirely fleshy; medial surface fused to medial head of M. flexor perforatus digiti III; deep surface fused to medial edge of underlying medial head of M. flexor perforatus digiti II; medial and lateral heads joined, forming bipinnate belly (pinnate structure most evident on deep surface); anterolateral head joined to distolateral part of belly.

Origin.—The *medial head* attaches fleshily to the proximal part of the popliteal area proximal (adjacent) to the origin of M. flexor hallucis longus and distolateral to the distal end of the origin of M. femorocruralis; the attachment extends laterally onto the posterolateral surface of the femur proximal (adjacent) to the common attachment of M. gastrocnemius pars externa and the distal arm of the guide loop for M. extensor iliofibularis; the medial edge of the origin is fused with part of the tendinous origin of the medial head of M. flexor perforatus digiti III.

The broad flat common tendon of the *lateral head* and the lateral head of

M. flexor perforatus digiti II fuses to the superficial surface of the fibular arm of the guide loop for M. extensor iliofibularis and contributes to the femorofibular fascia; consequently the ultimate origin would be the external femoral condyle and the head of the fibula.

The slender common tendon of the *anterolateral head* and the anterolateral heads of Mm. flexor perforatus digiti II and flexor perforatus digiti III passes deep to the insertional tendon of M. extensor iliofibularis and to the fibular arm of the guide loop for the latter muscle (to which it partly fuses); the tendon attaches to a narrow line on the head of the fibula adjacent to the attachment of the fibular arm of the guide loop and to the deep part of the femorofibular fascia.

INSERTION.—The slender ossified tendon becomes flexible before it passes posterior to the tibial cartilage deep to the tendon of M. gastrocnemius, lateral to the tendon of M. flexor perforans et perforatus digiti III, and superficial to the lateral half of the tendon of M. flexor perforatus digiti III; a thin sheet of connective tissue covers the tendon and attaches by its edges to the underlying tendon of M. flexor perforatus digiti III (thus the latter tendon forms a sheath for the tendon of M. flexor perforatus digiti IV; this sheath is separate from a similar sheath surrounding the tendon of M. flexor perforans et perforatus digiti III); the tendon is again ossified where it passes along the posterolateral surface of the tarsometatarsus posterolateral to the tendon of M. flexor perforans et perforatus digiti III; near the distal end of the tarsometatarsus the tendon becomes flexible and expands greatly in width and thickness, and sends a small slip dorsally, medial to the underlying tendons, that attaches to the subarticular cartilage ventral to the trochlea for digit IV; sometimes this slip is continuous with the retinaculum ventral to the tendon at the level of the proximal end of the digit. Several more or less distinct sheets of tough connective tissue lie ventral to all of the flexor tendons at the level of the trochleae and the proximal end of the digits, holding them in place. The tendon narrows as it passes onto the ventral surface of digit IV and soon divides into three branches; the tendon of M. flexor digitorum longus emerges between the medial and middle branches. The lateral branch attaches to the subarticular cartilage ventral to the first interphalangeal joint and is also bound by connective tissue to the ventrolateral surface of the first phalanx. A dorsal slip arises at the point of divergence of the lateral and middle branches and attaches to the subarticular cartilage of the first interphalangeal joint. The middle branch attaches to the subarticular cartilage of the second joint. The medial branch, after sending dorsal slips to each of the first two subarticular cartilages, attaches to the subarticular cartilage of the third interphalangeal joint.

INNERVATION.—The posterior division of the tibial nerve sends a branch into the posterior edge of the medial head, then passes between the latter and the medial head of M. flexor perforatus digiti III; as it extends distally it gives off twigs to the medial surface of the medial head, to the deep surface of the lateral head, and to the deep surface of the anterolateral head.

INDIVIDUAL VARIATION.—In one leg, an additional branch arises from the tibial nerve at the level of origin of the posterior division and enters the posterior surface of the medial head; a twig from this branch anastomoses with the first twig of the posterior division to the same head; a branch of the

medial division joins the posterior division distal to the origin of the twigs to the medial head but proximal to the origin of the twigs to the other heads.

T. cupido

Individual Variation.—None of significance.

P. p. jamesi

Individual Variation.—In four legs, a tiny vinculum connects with the tendon of M. flexor digitorum longus (which see).

M. Flexor Perforatus Digiti III, Figs. 13, 14, 15, 16, 17

T. pallidicinctus

General Description and Relations.—Divided into two widely separated heads—medial and anterolateral—with completely separate bellies but with common insertional tendon; small *anterolateral head* on lateral aspect of thigh deep to M. flexor perforans et perforatus digiti II and posterior to M. flexor digitorum longus; fleshy part of head distolateral to belly of M. flexor perforatus digiti IV; fleshy part fused to lateral edge of belly of M. flexor perforatus digiti II; proximal part of head a slender ossified tendon fused to anterior edge of both fleshy and tendinous parts of anterolateral head of M. flexor perforatus digiti IV and to lateral edge of anterolateral head of M. flexor perforatus digiti II; this tendon passing deep to tendon of insertion of M. extensor iliofibularis and to peroneal nerve; large *medial head* on posteromedial surface of thigh anterior to medial edge of M. gastrocnemius pars externa, lateral to M. gastrocnemius pars media, and medial to M. flexor perforatus digit IV; fused to medial surface of medial head of latter and to medial edges of Mm. flexor perforatus digiti II and flexor hallucis longus; proximal end of head tendinous.

Origin.—The *medial head* attaches tendinously to the medial part of the popliteal area in common with the medial head of M. flexor perforatus digiti II and with the medial edges of Mm. flexor perforatus digiti IV (medial head) and flexor hallucis longus; and is also fused to the articular capsule. The *anterolateral head* arises in common with the anterolateral heads of Mm. flexor perforatus digiti II and flexor perforatus digiti IV (see account of latter).

Insertion.—The short unossified tendon of the anterolateral head and the longer ossified tendon of the medial head join (after the latter becomes flexible) a short distance above the tibial cartilage, forming a broad flat common tendon that passes posterior to the tibial cartilage (in a shallow groove of the latter); the main part of the tendon is deep to the tendons of Mm. flexor perforatus digiti IV and flexor perforans et perforatus digiti III, but forms separate thin sheaths around these two tendons at the level of the tibial cartilage. A thin sheet of connective tissue covers these three tendons and attaches by its edges to the tibial cartilage, forming a sheath for them. These three tendons pass through the superficial groove in the hypotarsus deep to the tendon of M. gastrocnemius; the tendon of M. flexor perforatus digiti III is ossified for most of the length of the tarsometatarsus; a short distance below the hypotarsus, the anterior branch of the tendon of M. peroneus longus attaches broadly to the lateral edge of the tendon of M. flexor perforatus digiti III. In the proximal

part of the tarsometatarsus the tendon is deep to the tendon of M. flexor perforans et perforatus digiti III, but farther distally becomes medial and then superficial to the latter and lateral to the tendon of M. flexor perforans et perforatus digiti II; near the distal end of the tarsometatarsus a narrow but strong vinculum extends from the lateral edge of the tendon somewhat distally to the lateral edge of the tendon of M. flexor perforans et perforatus digiti III. At the distal end of the tarsometatarsus the tendon expands before entering the ventral surface of digit III where it soon divides into two branches, between which emerge the tendons of Mm. flexor perforans et perforatus digiti III and flexor digitorum longus; the lateral branch attaches to the subarticular cartilage ventral to the first interphalangeal joint and to the lateral surface of the distal end of the first phalanx; the medial branch has similar attachments on the medial side of the digit.

INNERVATION.—The posterior division of the tibial nerve passes between the medial heads of M. flexor perforatus digiti III and M. flexor perforatus digiti IV and sends a twig to the lateral surface of the former, then passes deep to the common belly of M. flexor perforatus digiti IV and sends a twig to the posterior surface of the anterolateral head of M. flexor perforatus digiti III.

INDIVIDUAL VARIATION.—None of significance.

T. cupido

INDIVIDUAL VARIATION.—In one leg, an extra branch (immediately distal to the branch to M. gastrocnemius pars media) of the medial division of the tibial nerve penetrates the medial surface of the proximal end of the medial head.

P. p. jamesi

INDIVIDUAL VARIATION.—None of significance.

M. Flexor Perforatus Digiti II, Figs. 15, 17

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Bipinnate; on posterior aspect of shank deep to M. flexor perforatus digiti IV and between two heads of M. flexor perforatus digiti III; bounded anteriorly by Mm. flexor digitorum longus and flexor hallucis longus; proximal part divided into three small heads—medial, lateral, and anterolateral; medial and proximal parts of *medial head* tendinous and extremely thin except for ossified medial edge; proximal part of *lateral head* tendinous and lateral to insertional tendon of M. extensor iliofibularis; both tendinous and fleshy parts fused to overlying tendon of M. flexor perforatus digiti IV; narrow *anterolateral head* fused to overlying anterolateral head of latter muscle and (anterolateral edge) to ossified tendon of anterolateral head of M. flexor perforatus digiti III; lateral edge of common belly fused to latter head; medial edge of muscle fused to medial heads of Mm. flexor perforatus digiti IV and flexor perforatus digiti III and to M. flexor hallucis longus.

ORIGIN.—The *medial head* attaches by a slender ossified tendon to the medial part of the popliteal area in common with the medial head of M. flexor perforatus digiti III and with the medial edges of Mm. flexor perforatus

digiti IV (medial head) and flexor hallucis longus; this head is also fused to the articular capsule. The above-mentioned ossified part of the tendon is situated at the junction of M. flexor perforatus digiti II and M. flexor perforatus digiti III (medial head) and could be considered to be a part of the latter rather than the former. The flat tendon of the *lateral head* arises in common with the lateral head of M. flexor perforatus digiti IV (which see). The *anterolateral head* arises in common with the anterolateral heads of Mm. flexor perforatus digiti IV and flexor perforatus digiti III (see former).

Insertion.—The short, slender, ossified tendon becomes flexible and passes through the canal in the tibial cartilage that lies medial to the canal for M. flexor hallucis longus and lateral to the canals for Mm. flexor digitorum longus and flexor perforans et perforatus digiti II. The tendon passes with the tendon of M. flexor perforans et perforatus digiti II (lateral to latter) through the canal in the hypotarsus that is deep to the groove for M. flexor perforatus digiti III and superficial to the canal for M. flexor digitorum longus; the former canal has a bony floor and sides but a fibrous roof; a fibrous partition subdivides the proximal half of this canal, forming a separate channel for each tendon. The tendon is ossified for most of the length of the tarsometatarsus and is situated lateral (adjacent) to the posterior metatarsal crest; immediately below the hypotarsus, the tendon becomes situated deep to the tendon of M. flexor perforans et perforatus digiti II and farther distally becomes situated medial and finally superficial to the latter; at the distal end of the tarsometatarsus the tendon expands greatly and its edges (thick) pass dorsally around the underlying flexor tendons and become continuous with the subarticular cartilage ventral to the trochlea for digit II. The tendon extends onto the ventral surface of digit II and attaches by its edges to the ventromedial and ventrolateral surfaces of the proximal part of the first phalanx (the lateral edge extending farthest distally); the tendons of Mm. flexor perforans et perforatus digiti II and flexor digitorum longus emerge from the distal end of the tendon of M. flexor perforatus digiti II.

Innervation.—The posterior division of the tibial nerve passes between the medial heads of Mm. flexor perforatus digiti III and flexor perforatus digiti IV and gives a twig to the superficial surface of each of the three heads of M. flexor perforatus digiti II and sometimes gives another twig to the superficial surface of the distal part of the common belly.

Individual Variation.—In one leg, a vinculum connects the tendon with that of M. flexor perforans et perforatus digiti II (which see).

T. cupido

Individual Variation.—The canal in the hypotarsus through which the tendon passes has a bony (instead of fibrous) roof in one leg.

P. p. jamesi

Individual Variation.—The variation given above for *T. cupido* is found in both legs of one specimen.

M. Flexor Hallucis Longus, Figs. 15, 19A

T. pallidicinctus

General Description and Relations.—Elongate and tapering; on posterior aspect of shank deep to M. flexor perforatus digiti II and to proximal end of medial head of M. flexor perforatus digiti IV; bounded anterolaterally by M. flexor digitorum longus and anteromedially by M. plantaris; tendinous anteromedial surface of proximal end fused to common tendon of origin of medial heads of Mm. flexor perforatus digiti III and flexor perforatus digiti II; belly ending approximately halfway down shank.

Origin.—The origin is fleshy and tendinous (anteromedial surface) from the popliteal area immediately distal to the origin of the medial head of M. flexor perforatus digiti IV, extending laterally to the area immediately proximal to the external femoral condyle (medial to the origin of M. gastrocnemius pars externa); the muscle also arises from the proximal end of the posterior part of the articular capsule.

Insertion.—The slender ossified tendon becomes flexible and passes through the canal in the tibial cartilage that lies lateral to the canal for M. flexor perforatus digiti II, then passes through a slight groove in the lateral surface of the hypotarsus and becomes ossified again; midway of the tarsometatarsus, the tendon becomes superficial to the tendon of M. flexor digitorum longus and is connected with the latter by an extensive vinculum, which extends from the deep surface and lateral edge of the tendon of M. flexor hallucis longus distally to the superficial surface of the tendon of M. flexor digitorum longus; the tendon continues, unossified and considerably reduced in size, distally medial to the tendon of M. flexor digitorum longus, and passes through the flexor groove of the first metatarsal anterolateral (adjacent) to the tendon of M. flexor hallucis brevis, then passes deep to the terminal expansion of the latter onto the ventral surface of the hallux; the tendon emerges from under the end of the tendon of M. flexor hallucis brevis and attaches to the ventral surface of the ungual phalanx; a weak dorsal slip attaching to the ventral surface of the distal end of the first phalanx is usually present.

Innervation.—A branch of the medial division of the tibial nerve passes along the medial edge of the muscle, giving several twigs into it.

Individual Variation.—None of significance in any of the three species studied.

M. Plantaris, Figs. 15, 19A

T. pallidicinctus

General Description and Relations.—Elongate and tapering; on posteromedial surface of tibiotarsus; bounded medially by M. gastrocnemius pars interna and tendon of M. flexor cruris medialis, posteriorly by M. gastrocnemius pars media and medial head of M. flexor perforatus digiti III, posterolaterally by M. flexor hallucis longus; medial to M. flexor digitorum longus; anterolateral surface of proximal end often slightly overlapping and fused to posterior surface of medial end of M. popliteus; belly terminating above middle of shank.

Origin.—The origin is fleshy and tendinous (distal edge only) from an elongate area on the posteromedial surface of the proximal end of the tibiotarsus adjacent to the insertion of M. popliteus.

INSERTION.—The long, slender, ossified tendon extends along the posteromedial aspect of the tibiotarsus and becomes flexible just before attaching to the proximomedial part of the tibial cartilage. The tibial cartilage is a large, mostly cartilaginous pad fitting closely over the posterior surface of the intratarsal joint; the distomedial corner is ossified. This cartilage is perforated by the tendons of several flexor muscles; the distal end of the cartilage attaches to the posteroproximal corner of the tarsometatarsus.

INNERVATION.—A branch of the medial division of the tibial nerve penetrates the lateral surface.

INDIVIDUAL VARIATION.—In one leg, a small bundle of fibers separates from the proximal end of the muscle, forming a short accessory head which attaches, separately from the remainder, to the articular capsule posteroproximal to the main origin; a blood vessel passes between the main and accessory heads.

T. cupido

INDIVIDUAL VARIATION.—In one leg, a small bundle of fibers arises from the medial collateral ligament. In another leg, the nerve to M. gastrocnemius pars interna passes through a gap in the origin of M. plantaris rather than distal to its origin.

P. p. jamesi

INDIVIDUAL VARIATION.—The nerve branch supplying M. gastrocnemius pars interna gives a minute twig to the deep surface of the free belly of M. plantaris in one instance.

M. Flexor Digitorum Longus, Figs. 14, 16, 17, 19A

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Relatively broad; bipinnate; on posterolateral surface of tibiotarsus; bounded posteromedially by M. flexor hallucis longus, posteriorly by M. flexor perforatus digiti II and anterolateral head of M. flexor perforatus digiti III, laterally by Mm. flexor perforans et perforatus digiti III and flexor perforans et perforatus digiti II, and anterolaterally by Mm. peroneus brevis and tibialis anticus; anterior surface of lateral part of distal half of common belly fused to M. peroneus brevis; divided into three heads—posterior (largest), lateral, and medial; *posterior head* on posterior surface of head of fibula; overlapping and fused to lateral end of M. popliteus; proximomedial corner deep to latter; *lateral head* on lateral surface of fibula; lateral and posterior heads separated by insertion of M. extensor iliofibularis; these two heads joined immediately distal to insertion of latter; *medial head* on posterior surface of tibiotarsus; group of blood vessels and nerves passing between medial and posterior heads; these two heads joined several mm. distal to junction of lateral and posterior heads; deep surface of insertional tendon near distal end of tarsometatarsus serving as origin for M. lumbricalis.

ORIGIN.—*Posterior head:* This arises fleshily from the posterior surface of the fibula beginning almost at the proximal end and from the medial surface of the fibula beginning deep to the distal part of M. popliteus. *Lateral head:* This arises fleshily (sometimes partly tendinously) from the lateral surface of the fibula proximal to the fibular tubercle. Some fibers arise from the distal

edge of the tendon of insertion of M. extensor iliofibularis. *Medial head:* This arises fleshily from the posterior surface of the tibiotarsus just medial to the distal part of the posterior head, distal to M. popliteus, and either lateral or distolateral to the origin of M. plantaris. Distal to the junction of the three heads, the muscle arises fleshily from the posterior surface of the tibiotarsus (except the distal part) and from the medial and posterior surfaces of the fibula.

Insertion.—The slender ossified tendon becomes flexible and passes through the canal in the tibial cartilage that lies anterolateral to the canal for M. flexor perforans et perforatus digiti II and anteromedial to the canal for M. flexor perforatus digiti II, then passes through the bony canal of the hypotarsus that is deep to all the other flexor tendons; the tendon ossifies again and lies adjacent (lateral) to the posterior metatarsal crest; the vinculum from the tendon of M. flexor hallucis longus fuses extensively to the superficial surface of the present tendon a short distance below the midpoint of the tarsometatarsus; the tendon is considerably broader below this point than above it. At the level of the first metatarsal, the tendon divides into three branches (unossified) that diverge, each passing through a groove on the ventral surface of the subarticular cartilages ventral to the trochleae, then pass onto the ventral surfaces of digits II, III, and IV. On *digit IV* the tendon gives off two dorsal fibro-elastic slips before attaching to the ventral surface of the ungual phalanx; one slip attaches to the subarticular cartilage ventral to the third interphalangeal joint, the other to the subarticular cartilage of the fourth joint and may also attach in part to the distal end of the fourth phalanx. On *digit III* the tendon gives off two dorsal slips before attaching to the ventral surface of the ungual phalanx; one slip attaches to the subarticular cartilage of the second interphalangeal joint, the other to the subarticular cartilage of the third joint and may also attach in part to the distal end of the third phalanx. On *digit II* the tendon gives off one dorsal slip before attaching to the ventral surface of the ungual phalanx; the slip attaches to the subarticular cartilage of the second interphalangeal joint and may also attach in part to the distal end of the second phalanx.

Innervation.—A branch of the medial division of the tibial nerve penetrates the medial surface of the posterior head.

Individual Variation.—In half the legs, the proximal end of the lateral head is notched for the passage of the peroneal nerve; the main part of the head lies medial to this nerve; the short fleshy slip lateral to this nerve arises by a long, slender, and extremely weak tendon from connective tissue surrounding the femorotibiotarsal joint. In one leg, a bundle of fibers separates from the lateral head and attaches to the terminal four mm. of the anterior (proximal) edge of the tendon of M. extensor iliofibularis. Each of the following variations occurs in several legs: a third dorsal slip on digit IV attaches to the distal end of the fourth phalanx in some legs and to the subarticular cartilage of the fourth joint in other legs; a third dorsal slip on digit III attaches to the distal end of the third phalanx in some legs and to the subarticular cartilage of the third joint in other legs; a second dorsal slip on digit II attaches to the distal end of the second phalanx in some legs and to the subarticular cartilage of the second joint in other legs.

T. cupido

Individual Variation.—The dorsal slips of insertion show variations similar to those noted above for *T. pallidicinctus*.

P. p. jamesi

Individual Variation.—In one leg, the proximal end of the lateral head is notched for the passage of the peroneal nerve. The dorsal slips of insertion show variations smiliar to those given above for *T. pallidicinctus*. In four legs, a tiny vinculum extends from the lateral edge of the branch of the tendon on digit IV to the lateral edge of the underlying medial branch of the tendon of M. flexor perforatus digiti IV at the level of the second phalanx.

M. Popliteus, Fig. 19B

T. pallidicinctus

General Description and Relations.—Extremely short but relatively broad and thick; on posterior surface of proximal end of tibiotarsus; extending distomedially from proximal part of fibula; deep to M. flexor hallucis longus; lateral end overlapped by, and fused to, posterior head of M. flexor digitorum longus; medial end often slightly overlapped by, and fused to, M. plantaris; medial end (insertion) much wider than lateral end (origin).

Origin.—The origin is fleshy and tendinous (superficial surface) from the medial surface of the fibula near the proximal end.

Insertion.—The attachment is fleshy to the posterior surface of the proximal end of the tibiotarsus adjacent (lateral) to the origin of M. plantaris.

Innervation.—A branch of the medial division of the tibial nerve penetrates the posterior surface.

Individual Variation.—None of significance in any of the three species studied.

M. Peroneus Longus, Figs. 12, 13

T. pallidicinctus

General Description and Relations.—Large; on anterolateral surface of shank; bounded medially by M. gastrocnemius pars interna and posterolaterally by Mm. flexor perforans et perforatus digiti III and flexor perforans et perforatus digiti II; proximal three fourths of posteromedial part (covered by M. gastrocnemius pars interna) aponeurotic and tightly fused to medial surfaces of underlying Mm. tibialis anticus and extensor digitorum longus; proximal part of fleshy belly somewhat fused to anterior surface of underlying M. tibialis anticus; posterolateral surface strongly fused to aponeurotic medial head of M. flexor perforans et perforatus digiti II and slightly fused to anterolateral edge of M. flexor perforans et perforatus digiti III.

Origin.—The muscle arises by fleshy and tendinous fibers from the edges of the inner and outer cnemial crests; the extreme proximal end arises either fleshily or aponeurotically from the rotular crest between the cnemial crests; the posteromedial edge (aponeurotic except distal one fourth fleshy) arises from the anteromedial intermuscular line.

Insertion.—The narrow ossified tendon on the superficial surface of the distal part of the fleshy belly extends several mm. beyond the belly where it

becomes flexible and divides into two branches. The short, broad posterior branch attaches broadly to the proximolateral corner of the tibial cartilage. The narrow anterior branch passes along the lateral surface of the tibiotarsus, through a strong retinaculum immediately proximal to the external condyle, and crosses the lateral surface of the joint, where it is covered by connective tissue nearly as tough as, and continuous with, the retinaculum; the tendon attaches broadly to the lateral edge of the ossified tendon of M. flexor perforatus digiti III a short distance below the hypotarsus.

INNERVATION.—The peroneal nerve sends twigs to the deep surface.

INDIVIDUAL VARIATION.—In both legs of two specimens, the extreme proximal end extends proximal to the rotular crest and attaches fleshily to the superficial surface of the distal end of the patellar tendon.

T. cupido

INDIVIDUAL VARIATION.—None of significance.

P. p. jamesi

INDIVIDUAL VARIATION.—One leg shows the variation described above for *T. pallidicinctus.*

M. Tibialis Anticus, Figs. 14, 15, 16, 19E, 20N

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Thick; on anterior aspect of thigh deep to M. peroneus longus; bounded posteriorly by M. extensor digitorum longus and posterolaterally by Mm. flexor digitorum longus and peroneus brevis; divided into two heads—tibial and femoral; small femoral head adjacent to posterolateral surface of much larger tibial head; two heads joined near midpoint of fleshy part of muscle, forming bipinnate belly (pinnate structure most evident on deep surface); proximal part of femoral head situated between outer cnemial crest and head of fibula; proximal part of anterior surface of tibial head somewhat fused to overlying M. peroneus longus; medial surface fused to aponeurosis of latter.

ORIGIN.—*Tibial head:* This arises by fleshy and tendinous fibers from the edge of the inner cnemial crest, from the rotular crest between the inner and outer cnemial crests, and from the anterior surface, distal edge, and posterior surface of the outer cnemial crest; the attachment may or may not extend onto the superficial surface of the distal part of the patellar tendon; the attachment is adjacent to the origin of the underlying M. extensor digitorum longus. *Femoral head:* This arises by a slender tendon from the notch in the distal end of the external condyle of the femur.

INSERTION.—The slender ossified tendon extends along the anterior surface of the distal end of the tibiotarsus and passes through a large, strong, oblique retinaculum (superficial to the supratendinal bridge); the lateral end of the retinaculum attaches to the lateral end of the supratendinal bridge; the medial end attaches immediately proximal to the medial end of the bridge. The tendon widens and becomes flexible as it passes across the anterior surface of the intratarsal joint, then narrows and attaches to the tubercle on the anterior surface of the proximal part of the tarsometatarsus between Mm. extensor hallucis longus and extensor brevis digiti IV. The

distalmost bundle of tendinous fibers does not attach to the tubercle, but extends distally along the anterior surface of the tarsometatarsus and attaches to the latter a few mm. distal to the tubercle, forming an accessory insertion. A part of the peroneal nerve passes between the main and accessory insertions.

INNERVATION.—A variable number of branches of the peroneal nerve penetrate the lateral surface of the femoral head; a variable number of branches of the same division pass deep to the femoral head and enter the posterior edge of the tibial head.

INDIVIDUAL VARIATION.—In one leg, the accessory insertion is absent.

T. cupido

INDIVIDUAL VARIATION.—None of significance.

P. p. jamesi

DIFFERENCES FROM TYPICAL *T. pallidicinctus*.—The origin of the tibial head does not extend onto the patellar tendon.

INDIVIDUAL VARIATION.—The accessory insertion is absent in one leg.

***M. Extensor Digitorum Longus*, Figs. 15, 17**

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Bipinnate; on anterior surface of tibiotarsus deep to M. tibialis anticus; bounded laterally by M. peroneus brevis; lateral edge usually slightly fused to proximal half of latter; medial surface fused to aponeurosis of M. peroneus longus.

ORIGIN.—The muscle arises fleshily from the lateral surface of the inner cnemial crest, from the rotular crest between the cnemial crests (deep to the attachment of M. tibialis anticus), from the basal (medial) half of the anterior surface of the outer cnemial crest, and from the anterior surface of the tibiotarsus (except the distal part) between the anteromedial and anterolateral intermuscular lines; proximal to the anterolateral intermuscular line, the origin usually extends almost to the lateral edge of the tibiotarsus.

INSERTION.—The ossified tendon extends along the mid-anterior surface of the distal part of the tibiotarsus deep to the tendon of M. tibialis anticus and passes under the supratendinal bridge, becoming flexible and widening slightly as it crosses the anterior surface of the intratarsal joint; the tendon narrows again and passes through a small but strong retinaculum on the anterior surface (medial to midline) of the proximal part of the tarsometatarsus; the retinaculum is immediately proximal and medial to the insertion of M. tibialis anticus. The tendon ossifies again as it passes down the anterior surface of the tarsometatarsus and bifurcates near the midpoint of the latter; the lateral branch soon bifurcates again; of these three branches, which are ossified for some distance, the lateral one passes onto the dorsal surface of digit IV, the middle one passes onto the dorsolateral surface of digit III, and the medial one subdivides (at the level of the trochleae) into three branches—one passing onto the dorsal surface of digit III and two passing onto the dorsal surface of digit II. At the level of the metatarsophalangeal joints, all of these tendons are interconnected by strong sheets of connective tissue and it is often difficult exactly to delimit the tendons at this level. On

the digits, tough connective tissue binds the tendons to the phalanges; this is most pronounced at the interphalangeal joints. The tendons are distinct on the first phalanx of each digit, but are often poorly defined farther distally. On *digit IV* the tendon subdivides into branches that attach to the proximal ends of the ungual, fourth, third, and (usually) second phalanges. On *digit III* the lateralmost tendon bifurcates, with one branch attaching to the ungual phalanx and the other to the proximal end of the third phalanx; the medial tendon attaches to the proximal end of the second phalanx. On *digit II* the originally medial tendon passes underneath and then lateral to the other tendon and attaches to the ungual phalanx; the other tendon attaches to the proximal end of the second phalanx.

INNERVATION.—One or more branches of the peroneal nerve enter the lateral edge.

INDIVIDUAL VARIATION.—In four legs, the lateral branch of the trifurcated tendon is not ossified at all.

T. cupido

INDIVIDUAL VARIATION.—In a few cases, the muscle does not come in contact with M. peroneus brevis.

P. p. jamesi

DIFFERENCES FROM TYPICAL *T. pallidicinctus*.—The belly is shorter. The lateral branch of the tendon on the tarsometatarsus is not ossified (true also of some legs of *Tympanuchus*).

INDIVIDUAL VARIATION.—In several legs, the muscle also arises from the distal part of the posterior surface of the outer cnemial crest.

M. Peroneus Brevis, Figs. 14, 16, 17, 18, 19A

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Small; on lateral surface of distal part of tibiotarsus; mainly anterior to fibula; bounded posteriorly and laterally by M. flexor digitorum longus (fused with latter), anteriorly by M. tibialis anticus, and anteromedially by M. extensor digitorum longus (usually slightly fused to latter).

ORIGIN.—The muscle arises by fleshy and tendinous fibers from the medial and anterior surfaces of the fibula beginning a short distance below the distal end of the fibular crest and from the anterolateral surface of the tibiotarsus anterior to the fibula; the anteromedial edge attaches to the anterolateral intermuscular line.

INSERTION.—The short, slender, ossified tendon passes along the anterolateral surface of the tibiotarsus and through a retinaculum immediately proximal and anteromedial to the retinaculum for the anterior branch of the tendon of M. peroneus longus; the tendon becomes flexible and widens as it passes across the lateral surface of the intratarsal joint deep to the tendon of M. peroneus longus, turning posteriorly and attaching to the proximolateral corner of the hypotarsus.

INNERVATION.—The superficial peroneal branch of the peroneal nerve gives one or two twigs to the anterior surface of the proximal part.

INDIVIDUAL VARIATION.—None of significance.

T. cupido

INDIVIDUAL VARIATION.—In a few legs, the muscle does not come in contact with M. extensor digitorum longus.

P. p. jamesi

INDIVIDUAL VARIATION.—None of significance.

M. Extensor Hallucis Longus, Figs. 19E, 20N

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Slender and elongate; proximal part on anterior surface of tarsometatarsus medial to anterior metatarsal groove; near midlength of tarsometatarsus, muscle twisted onto medial surface of latter; divisible into two heads—proximal and distal; belly of proximal head (largest) ending at level of twisting onto medial surface of bone; short distal head beginning at this point deep to tendon of proximal head and soon joining latter tendon.

ORIGIN.—*Proximal head:* This arises fleshily from the anterior surface of approximately the proximal half of the tarsometatarsus medial to the anterior metatarsal groove; the proximal end is partly medial to and partly deep to the retinaculum for M. extensor digitorum longus; some fibers arise from the extreme distal edge of the main insertion of M. tibialis anticus; the distal end of the belly is unattached. *Distal head:* This arises fleshily from the medial surface of the tarsometatarsus proximal to the first metatarsal and deep to the tendon of the proximal head.

INSERTION.—The slender tendon of the proximal head, which begins along the medial edge of the distal part of the belly, soon fuses with the superficial surface of the distal head (ossified here); the common tendon (unossified) passes onto the dorsal (proximal) surface of the first metatarsal, where it passes through a retinaculum, then passes along the dorsal surface of the hallux (bound by strong connective tissue to the metatarsophalangeal joint), attaching to the dorsal surface of the ungual phalanx.

INNERVATION.—The branch of the deep peroneal nerve that passes medial to the main insertion of M. tibialis anticus gives one or two twigs into the proximal part of the proximal head. No supply to the distal head was found, but see below.

INDIVIDUAL VARIATION.—In one leg, the proximal end of the distal head is fused to the distal end of the belly of the proximal head, whereas in three legs, a distinct gap separates the fleshy parts of the two heads. The following variations, each found in one leg, pertain to the relationship of the origin of the proximal head to the retinaculum for M. extensor digitorum longus: the origin does not extend proximally medial to the retinaculum; the origin does not extend proximally deep to this retinaculum; a part of the proximal end extends proximally lateral to this retinaculum (in this instance there is an unusually wide gap between the retinaculum and the insertion of M. tibialis anticus). In one leg, the distalmost fibers of the distal head do not join the common tendon but insert independently on the articular capsule of the metatarsophalangeal joint (deep to the common tendon).

T. cupido

INDIVIDUAL VARIATION.—The relationship between the two heads varies as follows: the proximal end of the distal head may be fused to the distal end of the belly of the proximal head; the proximal end of the distal head may begin anterior (adjacent) to the distal end of the belly of the proximal head; there may be a distinct gap between the fleshy parts of the two heads. In two legs, there is no origin from the insertion of M. tibialis anticus. In one leg, a small accessory bundle of fleshy fibers arises from the proximal end of the first metatarsal (widely separated from the origin of the distal head), passes through the retinaculum deep to the common tendon and attaches to the dorsal surface of the articular capsule of the metatarsophalangeal joint; thus this bundle is completely separate from the remainder of the muscle. In two legs, the same nerve branch that gives twigs into the proximal head also gives off (much farther distally) a twig that enters the distal head.

P. p. jamesi

INDIVIDUAL VARIATION.—The proximal end of the distal head may begin anterior (adjacent) to the distal end of the belly of the proximal head. In four legs, the origin of the proximal head does not extend proximally medial to the retinaculum for M. extensor digitorum longus; in one of these legs, a part of the proximal end extends proximally lateral to this retinaculum. The distalmost fibers of the distal head do not join the common tendon but insert independently on the dorsal surface of the articular capsule of the metatarsophalangeal joint in four legs; in another leg, the entire distal head has the latter insertion (consequently the two heads are completely separate).

M. Abductor Digiti II, Figs. 19E, 20N

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Short; on medial surface of distal part of tarsometatarsus; proximal end adjacent (anterior) to distal head of M. extensor hallucis longus.

ORIGIN.—The origin is fleshy from the medial surface of the distal part of the tarsometatarsus anterior (adjacent) to the first metatarsal and from the anteromedial surface of the basal half of the first metatarsal.

INSERTION.—The flat tendon passes over the medial surface of the trochlea for digit II and attaches to the medial surface of the proximal end of the first phalanx of digit II; the tendon is fused with the articular capsule.

INNERVATION.—The compound nerve formed by the fusion of a branch of the superficial peroneal nerve with a branch of the deep peroneal nerve gives a twig to the anterolateral edge of the muscle.

INDIVIDUAL VARIATION.—In some cases, the twig arises from the deep peroneal branch alone (which is not joined by the superficial peroneal nerve).

T. cupido

INDIVIDUAL VARIATION.—In one leg, some of the fleshy fibers arising from the first metatarsal insert independently on the medial surface of the trochlea for digit II (deep to the main part of the muscle).

P. p. jamesi

INDIVIDUAL VARIATION.—None of significance.

M. Extensor Brevis Digiti III (M. extensor proprius digiti III), Figs. 19E, 20N

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Short and relatively broad (narrow proximally); on mid-anterior surface of distal part of tarsometatarsus; tendon of insertion fused with articular capsule.

ORIGIN.—The origin is fleshy from the mid-anterior surface of the distal part of the tarsometatarsus ending a short distance proximal to the trochlea for digit III.

INSERTION.—The flat tendon passes over the trochlea for digit III and attaches to the dorsal surface of the proximal end of the first phalanx of digit III.

INNERVATION.—The compound nerve formed by the fusion of a branch of the superficial peroneal nerve with a branch of the deep peroneal nerve gives a twig to the proximal end of the muscle.

INDIVIDUAL VARIATION.—In some cases, the twig arises from the deep peroneal branch alone (which is not joined by the superficial peroneal nerve). The individual variation is insignificant in *T. cupido* and *P. p. jamesi*.

M. Extensor Proprius Digiti III (Not found by Hudson, *et al.*), Fig. 20N

T. pallidicinctus and *T. cupido*

Absent in both species.

P. p. jamesi

This atypical muscle was found in only two legs (P.p. 1L and 4L). The following description applies to P. p. 4L (Fig. 20N).

GENERAL DESCRIPTION AND RELATIONS.—Small but well developed; fleshy part 1½ × 13 mm.; proximal end narrower; on mid-anterior surface of tarsometatarsus between Mm. extensor brevis digiti IV and extensor hallucis longus and mostly proximal to M. extensor brevis digiti III; tendinous distal part superficial to latter; fleshy belly ending immediately distal to proximal end of latter.

ORIGIN.—The origin is fleshy from a narrow elongate area on the mid-anterior surface of the tarsometatarsus between Mm. extensor brevis digiti IV and extensor hallucis longus, beginning at the distal end (bony) of the elongate accessory insertion of M. tibialis anticus. The distal part of the belly is free.

INSERTION.—The attachment is by a thin, wide (relative to belly) tendon to the superficial surface of M. extensor brevis digiti III.

INNERVATION.—Not found.

INDIVIDUAL VARIATION.—In P.p. 1L, the muscle is less well developed. The fleshy belly is 1 × 5 mm. It arises from the lateral edge of M. extensor hallucis longus. The extremely slender insertional tendon attaches as above.

M. Extensor Brevis Digiti IV, Figs. 19E, 20N

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Slender and tapering; on lateral part of anterior surface of tarsometatarsus; length of belly variable; middle of medial edge in contact with M. extensor hallucis longus.

ORIGIN.—The origin is fleshy from the lateral part of the anterior surface of the tarsometatarsus, including the anterior metatarsal groove.

INSERTION.—The long slender tendon enters the anterior aperture of the distal foramen, passes through the intertrochlear canal, emerges from the terminal foramen, and attaches to the medial surface of the proximal end of the first phalanx of digit IV.

INNERVATION.—The superficial peroneal branch of the peroneal nerve sends a twig into the proximal part of the muscle.

INDIVIDUAL VARIATION.—None of significance in any of the three species studied.

M. Lumbricalis, Fig. 19F

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Small, thin, and strap-shaped; on mid-posterior surface of distal end of tarsometatarsus deep to tendon of M. flexor digitorum longus; belly partly fleshy and partly elastic connective tissue.

ORIGIN.—The muscle arises from the deep (anterior) surface of the tendon of M. flexor digitorum longus a short distance proximal to the trifurcation of the latter.

INSERTION.—The muscle attaches to the proximal end of the subarticular cartilage ventral to the trochlea for digit III.

INNERVATION.—A long but extremely small twig arises from the paraperoneal branch of the tibial nerve a short distance distal to the hypotarsus and extends distally along the mid-posterior surface of the tarsometatarsus (parallel to a larger nonmuscular branch) and enters the deep surface distal to the middle. It was possible to follow this twig in only two legs; it was presumably destroyed in the course of dissection in the others.

INDIVIDUAL VARIATION.—In some cases, the "muscle" appears grossly to be entirely connective tissue, although a distinct entity.

T. cupido

INDIVIDUAL VARIATION.—In some cases, the "muscle" appears grossly to be entirely connective tissue. The innervation was found in only one leg, in which the twig arises more distally than in *T. pallidicinctus.*

P. p. jamesi

The innervation was not found.

M. Abductor Digiti IV, Fig. 19F

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Slender and elongate; on posterior surface of tarsometatarsus lateral to midline; in contact with M. flexor hallucis brevis in midline.

ORIGIN.—The origin is fleshy from the posterior surface of the tarsometatarsus lateral to the midline beginning near the proximal end (lateral to the hypotarsus) and ending at the level of the first metatarsal.

INSERTION.—The slender tendon, which begins along the lateral edge of the distal part of the belly, passes through a retinaculum on the posterolateral surface of the tarsometatarsus immediately above the outer trochlea and attaches to the lateral surface of the proximal end of the first phalanx of digit IV.

INNERVATION.—The paraperoneal branch of the tibial nerve gives one or two twigs to the proximal part of the muscle.

INDIVIDUAL VARIATION.—None of significance in any of the three species studied.

M. Flexor Hallucis Brevis, Fig. 19F

T. pallidicinctus

GENERAL DESCRIPTION AND RELATIONS.—Slender and elongate; on posterior surface of tarsometatarsus medial to midline; belly (except proximal end) adjacent (lateral) to posterior metatarsal crest; proximal end passing under latter (immediately distal to hypotarsus) and lying anteromedial to hypotarsus.

ORIGIN.—The origin is fleshy from the medial metatarsal depression and from the posterior surface of the tarsometatarsus between the midline and the posterior metatarsal crest beginning immediately below the hypotarsus and ending a short distance above the first metatarsal (sometimes more proximally).

INSERTION.—The slender tendon, which begins along the medial edge of the distal part of the belly, passes through the groove on the posterodistal surface of the first metatarsal and onto the proximal end of the ventral surface of the hallux; the tendon widens considerably and attaches by its edges to the ventral surface of the proximal end of the first phalanx, forming a short "tunnel" through which the tendon of M. flexor hallucis longus passes.

INNERVATION.—The paraperoneal branch of the tibial nerve sends one or two twigs into the proximal part of the muscle (but distal to the hypotarsus).

INDIVIDUAL VARIATION.—In two legs, the muscle arises in part from the distal end of the lateral calcaneal ridge. The individual variation is insignificant in *T. cupido* and *P. p. jamesi.*

DISCUSSION AND CONCLUSIONS

Analysis of Individual Variation

Considerable individual variation occurs in both the muscles and the nerves of the leg of the three species studied. The amount of variation reported by a worker depends in large part on the degree of variation that he considers significant.

Individual variation in the muscles and in the nerves will be discussed separately; that of the muscles (excluding innervation) will be considered first.

Muscles

Considering the number, rather than degree, of variations, the most variable muscles are: Mm. flexor digitorum longus, obturator, caudofemoralis, and extensor hallucis longus. The first-mentioned muscle exhibits 14 different variations in the specimens studied. Mm. vastus lateralis, flexor perforans et perforatus digiti II, and piriformis also showed a considerable number of variations. The following muscles did not exhibit any variations considered significant in this study: Mm. vastus medialis, femoritibialis internus, flexor perforatus digiti III, extensor brevis digiti III, and abductor digiti IV.

Muscles showing a great *degree* of individual variation included the following: M. extensor proprius digiti III was present in two legs of *Pedioecetes* but absent in the other legs studied. A fleshy muscle slip connected M. caudofemoralis pars caudifemoralis with the tendinous raphe between Mm. flexor cruris lateralis and femorocruralis in two legs, whereas in others this connection was tendinous or even absent altogether. M. caudofemoralis pars caudifemoralis had a tendinous area within the belly in only three legs. A vinculum connected the insertional tendons of Mm. flexor perforans et perforatus digiti II and flexor perforatus digiti II in only one leg. The fleshy belly of M. iliotrochantericus medius was completely split into two parts in one leg. M. flexor cruris lateralis had an accessory slip arising from the caudal musculature in one leg.

Certain individual variations reported in the accounts of the muscles formed a graduated series, as far as degree is concerned, from the typical to the extreme condition. Therefore it was difficult or impossible in some cases to state whether or not certain specimens exhibited such a variation. Elimination of the doubtful instances of variation leaves a total of 50 different variations (excluding variations between species) which can be attributed to a definite number of specimens. The remainder of the discussion of individual variation in the muscles concerns these 50 variations. See table 3.

The typical condition of any structure is considered to be the condition of that structure in the majority of the legs studied. Some conditions considered as typical in the present study might not be so considered if a larger number of specimens had been studied. If exactly half of the legs of one species shows a particular condition

of a structure, the condition typical for this species is considered (for purposes of the following discussion) to be that found in the majority of the legs of the other species.

In all instances except two (of 50) the typical condition of the muscles in *T. pallidicinctus* was also the typical condition in *T. cupido*. The majority of the legs in *T. cupido* had an additional dorsal slip on the tendon of M. flexor digitorum longus in digits II and III. In all instances except seven the typical condition in *T. pallidicinctus* was also the typical condition in *Pedioecetes*. In these seven instances a variation in the former was the typical condition in the latter. These were: an additional dorsal slip on the tendon of M. flexor digitorum longus in each of three digits, a vinculum between the latter and M. flexor perforatus digiti IV, a partly fleshy insertion of M. flexor cruris medialis, an unossified lateral branch of the insertional tendon of M. extensor digitorum longus, and an independent insertion of the distalmost fibers of the distal head of M. extensor hallucis longus. For all characters except the number of the dorsal slips on the tendon of M. flexor digitorum longus in digits II and III, the typical condition in *T. pallidicinctus* was also the typical condition for all species considered together. To facilitate comparison, in the following discussion all of the above-mentioned characters are considered in all species as variants from the typical condition.

Certain legs showed a greater number of variations from the typical condition than did others. The majority of legs showed from four to seven variations in the muscles of the leg. The extremes were P.p. 1L, which showed 11, and T.c.p. 2L, which exhibited only one variation.

Twenty-three of the 50 variations were found in only one leg (out of 23). It would be expected that if additional specimens were studied, more kinds of variations would be found. Nine variations were found in only two legs, five in three legs, five in four legs, and four in five legs. One variation was found in nine legs, one in ten legs, and two in 12 legs; the last four variations were in the number of dorsal slips of the insertional tendon of M. flexor digitorum longus in digits II, III, and IV and in the ossification of the insertional tendon of M. extensor digitorum longus.

Five of the variations were found only in specimens in which only one leg was dissected. Considering only those eight specimens in which both legs were dissected, five of the 45 variations were found in both legs of each specimen exhibiting the variation;

28 variations were found in only one leg of each specimen exhibiting the variation; 12 variations were found in both legs of some specimens but in only one leg of other specimens. Of the six muscle features showing the greatest degree of individual variation (described previously), only two (both pertaining to M. caudofemoralis) were found in both legs of the specimens exhibiting the variation.

For one leg (the one showing the most variations) of each specimen of which both legs were studied, the number of variations that this leg had in common with every other leg (of all species) was determined. Then the number of variations in common between the two legs of one individual was compared with the number of variations in common between one leg of this individual and each leg of every other individual. See table 4. One leg of six of the eight specimens showed at least as many variations in common with a leg of another individual as with the other leg of the same individual. The two exceptions were T.p. 2R and T.c.a. 1R. Thus for most specimens there was as much variation in the muscles between the right and left legs of one individual as there was between individuals.

Of the 50 muscle variations seven were found only in *T. pallidicinctus* (eight legs), 16 were found only in *T. cupido* (nine legs), and ten were found only in *Pedioecetes* (six legs). Two were found in both species of *Tympanuchus* (but not in *Pedioecetes*). Fifteen were found in both *Tympanuchus* and *Pedioecetes*; of these, five were found in all three species studied, eight were shared by *T. pallidicinctus* and *Pedioecetes*, and two occurred in *T. cupido* and *Pedioecetes*.

Nerves

The lumbosacral plexus, femoral nerve, sciatic nerve, and tibial nerve all showed numerous individual variations. The peroneal nerve, however, was relatively constant. Variations in the obturator nerve were considered to be insignificant. See table 5.

In all instances except one (of 40) the typical condition in *T. pallidicinctus* was also the typical condition in *T. cupido*. In most of the legs of the latter the nerve to M. flexor cruris lateralis did not perforate M. caudofemoralis. In all instances except four the typical condition in *T. pallidicinctus* was also the typical condition in *Pedioecetes*. These exceptions were: prefixation of the lumbosacral plexus, six roots of the sciatic nerve, femoral nerve formed mainly from S2 to S4 and two twigs to M. flexor ischiofemoralis.

In all instances the typical condition in *T. pallidicinctus* was also the typical condition for all species considered together.

Certain legs showed a greater number of variations from the typical condition of the nerves than did others. The greatest number of variations was shown by P.p. 3L, which had 12. T.p. 1R and T.c.p. 1L both showed only one.

All six variations in the lumbosacral plexus were found on both sides of each specimen exhibiting the variation. In marked contrast to the other nerves, there was no significant variation in the lumbosacral plexus between the right and left sides of one individual. (This might not always be true, however, if a larger number of specimens were studied.) Of the variations in the lumbosacral plexus, one was found in only one specimen (of 15), one was found in three specimens, one in four specimens, two in six specimens, and one in seven specimens. Of the 34 variations found in the other nerves, 14 were found in only one leg (of 23), six occurred in two legs, four in three legs, three in four legs, three in five legs, two in six legs, one in seven legs, and one in nine legs.

Four of the variations were found only in specimens in which only one leg was dissected. Considering only those eight specimens in which both legs were dissected, and excluding the lumbosacral plexus, ten of the 30 variations were found in both legs of each specimen exhibiting the variation; 16 variations were found in only one leg of each specimen exhibiting the variation; four variations were found in both legs of some specimens but in only one leg of other specimens.

The number of variations in common between the two legs of one individual was compared with the number between individuals in the same manner as for the muscles; the lumbosacral plexus was excluded from consideration. See table 6. One leg of six of the eight specimens showed at least as many variations in common with a leg of another individual as with the other leg of the same individual. The two exceptions were T.p. 2L and T.p. 3R. Thus for most specimens there was as much variation in the nerves other than the lumbosacral plexus between the right and left legs of one individual as there was between individuals.

Of the 40 nerve variations (including the lumbosacral plexus) 11 were found only in *T. pallidicinctus,* seven were found only in *T. cupido,* and seven were found only in *Pedioecetes.* Four were found in both species of *Tympanuchus* (but not in *Pedioecetes*). Eleven were found in both *Tympanuchus* and *Pedioecetes;* of

these, four were found in all three species, three were shared by *T. pallidicinctus* and *Pedioecetes*, and four occurred in *T. cupido* and *Pedioecetes*.

The average number of variations per leg in both muscles and nerves was 11 in *T. pallidicinctus*, nine in *T. cupido*, and 16 in *Pedioecetes*. The high number in the last is in part the result of these being variations from the typical condition of *T. pallidicinctus* (rather than from *Pedioecetes*).

Analysis of Variation Between Species

No constant differences in the muscles or nerves was found between *T. cupido pinnatus* and *T. cupido attwateri*. Only one constant difference was found between *T. cupido* and *T. pallidicinctus*: a thicker fleshy origin of M. extensor iliotibialis lateralis in *T. cupido* (associated with a thicker edge of the lateral iliac process).

Although no constant differences in the nerves were found between *Pedioecetes* and *Tympanuchus* (both species), 17 constant differences in the muscles were found between these two genera. Seven of these differences pertain to features of a single muscle—M. flexor cruris medialis. Compared with the condition in *Tympanuchus*, M. flexor cruris medialis in *Pedioecetes* has a wider origin, a partly fleshy (instead of entirely tendinous) origin, a more pronounced curvature of the line of origin, a wider insertion, an insertion posterior (rather than anterior) to the medial collateral ligament, an insertion that attaches in part to the articular capsule, and a shorter tendon of insertion (resulting in the fusion of the common insertional tendon of Mm. flexor cruris lateralis and femorocruralis with the fleshy belly rather than with the insertional tendon). Other differences include the following. A more extensive posteroproximal aponeurosis of M. extensor iliotibialis lateralis in *Pedioecetes* (resulting in a narrower fleshy origin); a more nearly straight line of origin of this muscle (associated with a less pronounced lateral iliac process); a thinner fleshy origin of this muscle (associated with a thinner edge of the lateral iliac process); a wider M. flexor cruris lateralis that is fleshy up to the origin from the vertebrae; a wider fleshy origin of M. iliacus; the origin of M. caudofemoralis pars iliofemoralis not reaching the ventral edge of the ischium; a narrower origin of M. adductor superficialis; a wider M. femorocruralis; and a shorter belly of M. extensor digitorum longus. Some additional differences between these two genera, which are slight in degree, are given in the ac-

counts of the muscles. If additional specimens were studied, some of the differences listed above possibly would prove to be subject to individual variation and so could not properly be listed as constant differences between the two genera.

The picture of the differences between *Tympanuchus* and *Pedioecetes* that the present study presents is radically different from that presented by the study of Hudson, *et al.* (1959). These authors reported the following differences between these two genera. (I am using my terminology.) The origin of M. piriformis is narrower in *Pedioecetes* and is more posteriorly situated; the belly of M. extensor iliotibialis anticus is broader in *Pedioecetes*; the belly of M. tibialis anticus is longer; the belly of M. peroneus brevis is shorter; the insertional tendon of the anterolateral head of M. flexor perforatus digiti III is shorter; the belly of M. flexor digitorum longus is shorter; only two (rather than three) of the branches of M. extensor digitorum longus on the tarsometatarsus are ossified; the posterior metatarsal crest is shorter; M. flexor perforans et perforatus digiti II has two heads in *Pedioecetes* but only one in *Tympanuchus*; the roof over the hypotarsal canal enclosing the tendon of M. flexor digitorum longus is bony in *Pedioecetes* but fibrous in *Tympanuchus;* M. flexor cruris lateralis is wider in *Pedioecetes*; and the origin of M. femorocruralis is wider. I paid particular attention in my study to these 13 features given by Hudson, *et al.*; of these the only differences that I found to be constant were the last two. The apparent reason for this great discrepancy is the small number of legs of *Tympanuchus* studied by Hudson, *et al.* They studied eight legs of *Pedioecetes* but only two legs of *Tympanuchus.* This emphasizes the danger of making comparisons based on a very small number of specimens (a criticism which may prove to apply to the present study as well). The reason why Hudson, *et al.* did not report most of the differences found by me is not so apparent. Either the specimens studied by the former workers showed a greater variation in these characters than did my specimens or else those workers overlooked the differences. Probably both factors are involved. It remains to be determined how many specimens need to be studied in order to obtain a fairly accurate picture of variation.

Comparison with Other Studies of Innervation

I accept the following concept of muscle-nerve relationship. All muscles of the pelvic limb of birds have developed phylogenetically

from either the dorsal extensor muscle mass or the ventral flexor muscle mass. The former was (at least originally) supplied by only the femoral and peroneal nerves ("dorsal" nerves), the latter by only the obturator and tibial nerves ("ventral" nerves). The best guide for determining which muscles are phylogenetically dorsal and which are ventral seems to be their embryogeny (as shown in the studies of Romer, 1927, and Wortham, 1948). In the phylogenetic changes undergone by the muscles under consideration, the innervation may have changed in some instances, although this is less likely to occur than changes in the attachment or function of the muscles. If a change in innervation has occurred, it would be more likely to be a change from one dorsal nerve to the other or from one ventral nerve to the other rather than from a dorsal nerve to a ventral one or *vice versa.*

Thus, in my opinion, a report of a dorsal muscle supplied by a ventral nerve, or *vice versa,* should be viewed with suspicion until it is verified. I suspect that many previous workers have ignored this concept of muscle-nerve relationship, or else do not accept it, since they report, without comment, dorsal muscles (as determined embryologically) innervated by ventral nerves, or *vice versa.* Owing to the intimate association between the proximal parts of the tibial and peroneal nerves, the true relationship may be difficult to determine. I suspect that this relationship has been misinterpreted by a number of workers. I found in *Tympanuchus* and *Pedioecetes* a branch of the tibial nerve that is closely associated with, and distributed with, the peroneal nerve and has been mistakenly considered a part of the peroneal nerve by some workers. In the study here reported on, I have found no definite exceptions to the expected innervation. The only possible exception is an extra branch, which could not be traced to its origin, supplying M. extensor iliofibularis in one leg. Thus my study of innervation agrees with the embryological determination of the (phylogenetic) dorsal and ventral muscles and lends strong support to the above-stated concept of muscle-nerve relationship.

I have compared my findings on the nerves with those of other workers, who have studied the nerves with a varying degree of thoroughness. The important differences in innervation between these studies and the present one are discussed below.

In neither of Gadow's works did he distinguish tibial and peroneal components in the thigh. In his later work (1891), covering a wide variety of birds, he found that M. piriformis sometimes has

a femoral innervation in addition to the constant sciatic one and that M. gluteus profundus may or may not have a sciatic supply in addition to the femoral one. A comparison of Gadow's terminology of the sciatic nerve branches in the shank and foot (in both works) with mine shows that his branch I represents my peroneal nerve plus my paraperoneal branch of the tibial nerve (Ic); his branch II represents my medial division of the tibial nerve; and his branch III represents my posterior (IIIa) and lateral (IIIb) divisions of the tibial nerve.

Gadow's study (1880) on the ratites included *Struthio, Rhea,* and *Casuarius.* Only in *Casuarius* did Gadow find a branch (IIe) of the sciatic nerve supplying Mm. lumbricalis, adductor digiti II, and abductor digiti II. The two former muscles are typically supplied (as in *Rhea*) by the paraperoneal branch of the tibial nerve; Gadow's branch IIe presumably represents a segregated branch of this nerve. More surprising is his finding that M. abductor digiti II is innervated in *Casuarius* by both the deep peroneal nerve and branch IIe and in *Rhea* by branch Ic (paraperoneal branch of tibial nerve). The deep peroneal innervation is typical. Also unexpected is his finding that the posterior division of the femoral nerve gives minute twigs into M. gastrocnemius pars interna in *Struthio* and *Casuarius.* Since the other terminal branches of this nerve in these birds are nonmuscular, since this muscle is chiefly supplied by other nerves, and since the innervation from the femoral nerve is apparently atypical for most birds, the possibility should be considered that the femoral twigs are sensory rather than motor.

Sudilovskaya (1931), studying *Struthio, Rhea,* and *Dromaeus* (*Dromiceius*), used the same terminology as Gadow except that he designates as branch III Gadow's branch Ic. Sudilovskaya's discussion of the main branches of the sciatic nerve is confusing. He states that in *Struthio,* branches I, II, and III all pass through the tendinous guide loop for M. extensor iliofibularis; this is hard to believe. As near as I can determine, he has mistakenly given the same designation (branch III) to two separate branches (Gadow's Ic and III). There is no problem, however, in determining to which of these two branches he is referring when he is describing the innervation of a particular muscle, since one supplies only muscles of the shank and the other only intrinsic foot muscles. Sudilovskaya found M. abductor digiti II to be innervated by branch III (Ic of Gadow); thus the innervation of this muscle corresponds to that found in *Rhea* by Gadow. Although M. adductor digiti II had the expected innervation from branch III (paraperoneal branch of

tibial nerve) in *Dromaeus,* that muscle was found to be supplied by branch II in *Rhea.* (Gadow, on the other hand, reports a typical innervation for this muscle in *Rhea.*) Sudilovskaya found M. peroneus brevis to be supplied by the deep peroneal branch (in contrast to the superficial peroneal supply that I found in *Tympanuchus* and *Pedioecetes*). He found M. gastrocnemius pars interna to be supplied in *Struthio* by twigs of the femoral nerve in addition to its typical innervation from branch II of the sciatic nerve; this agrees with Gadow's findings in the same genus. Sudilovskaya reports that M. gastrocnemius pars externa was innervated by branches II and III in *Struthio* and *Rhea* and by branches I and III in *Dromaeus.* (Gadow found only the typical innervation—branch III.)

In the Whooping Crane, Fisher and Goodman (1955) found a peroneal, rather than a femoral, nerve supply for pars postica of M. vastus lateralis. They also report a peroneal nerve supply for M. flexor ischiofemoralis (in contrast to the usual tibial nerve supply) and for M. adductor superficialis (in addition to the usual supply from the obturator nerve). The innervation was not given for the intrinsic foot musculature.

Fisher (1946), studying vultures, reports the following: tibial branches, in addition to the main sciatic branch, supplying M. extensor iliofibularis (typically supplied by the peroneal nerve); an obturator supply, in addition to the usual tibial supply, to M. flexor cruris medialis; a tibial supply, in addition to the typical obturator supply, to M. obturator pars postica; a possible obturator supply, in addition to the typical femoral supply, to M. ambiens; a possible peroneal supply, in addition to the typical tibial supply, to M. flexor digitorum longus; and a peroneal supply to Mm. abductor digiti IV, flexor hallucis brevis, and adductor digiti II (which are typically supplied by the paraperoneal branch of the tibial nerve). Fisher's postfibular branch of the peroneal nerve, which supplies the latter three muscles, apparently represents the paraperoneal branch of the tibial nerve.

Carlsson (1884) did not find a femoral nerve supply for M. gluteus profundus. He found an obturator supply, in addition to the usual sciatic supply, to M. flexor ischiofemoralis in *Eudyptes chrysolopha* and *Mergulus alle* but not in the other two forms studied. He reported a peroneal supply, rather than the expected tibial (paraperoneal) supply, to Mm. abductor digiti IV and adductor digiti IV.

DeMan (1873) found a twig of the obturator nerve supplying

M. flexor ischiofemoralis, in addition to the typical innervation, in *Corvus monedula,* but not in the few other forms studied. He did not distinguish tibial and peroneal components in the thigh.

Wilcox (1948), studying a loon, did not find any peroneal supply to M. extensor iliotibialis lateralis or to M. gluteus profundus. He found a femoral, rather than a peroneal, supply to M. piriformis. He found an obturator, instead of a tibial, supply to M. flexor ischiofemoralis. (In some of my specimens I found a tiny blood vessel, appearing much like a nerve, emerging from the obturator foramen and entering M. flexor ischiofemoralis.) Wilcox reports an innervation of M. caudofemoralis pars caudifemoralis from the pudendal plexus, in addition to the usual sciatic one. Wilcox did not distinguish tibial and peroneal components in the thigh. In the shank and foot he misidentified the peroneal nerve as the tibial nerve and therefore gave erroneous innervations for all the muscles supplied by this nerve, except for M. adductor digiti IV, which actually should be supplied by the tibial nerve.

Howell (1938) studied only the hip and thigh musculature of the chicken. He overlooked the femoral nerve supply for M. gluteus profundus.

Romer (1927) studied only the hip and thigh muscles of the chick. He did not distinguish tibial and peroneal components in the thigh. He did not mention any sciatic supply for M. gluteus profundus.

Appleton (1928), studied (in various birds) only those muscles of the hip and thigh that are innervated by the tibial and peroneal nerves. He terms the former "ischiadicus ventralis" and the latter "ischiadicus dorsalis." His findings did not differ from mine.

Many differences in the innervation of specific muscles are reported in the literature, even in the same species (by different workers). Some of these differences may be real; others are probably misinterpretations. Consequently more work needs to be done before a complete understanding can be obtained of the innervation of the leg muscles of birds. Especially needed are studies of the tibial-peroneal nerve relationship, perhaps approached by a method other than gross dissection.

SUMMARY

The muscles and nerves were dissected in eight legs of the Lesser Prairie Chicken (*Tympanuchus pallidicinctus*), six legs of the Greater Prairie Chicken (*T. cupido pinnatus*), three legs of Attwater's Prairie Chicken (*T. c. attwateri*), and six legs of the Sharp-tailed Grouse (*Pedioecetes phasianellus jamesi*) for the purpose of obtaining information on individual variation as well as variation between these closely related species. Relatively little information is available regarding the nerves of the leg of birds and little is known about individual variation and variation between closely related forms in the muscles of the leg of birds.

All osteological terms used in the present paper are defined and those of the pelvis are illustrated. New terms were coined for some structures for which no names could be found in the literature. Terms were also coined for the major divisions of the femoral and sciatic nerves. With three exceptions, my muscle terminology follows that of Fisher (1946) and Fisher and Goodman (1955). Their term femoritibialis externus is not used here; the muscle so named is considered to be a part of M. vastus lateralis. Fisher's accessory head of M. flexor cruris lateralis is considered to be a distinct muscle —M. femorocruralis. Usage of the term obturator internus is avoided because the muscle so named is considered not to be homologous with the mammalian muscle of the same name; the entire obturator complex is called M. obturator, and is subdivided into four parts.

The typical (most common) condition of the nerves and muscles in *Tympanuchus pallidicinctus* is described in detail. Variations from this condition among the other birds studied are then described. All muscles of one leg of *T. pallidicinctus* are illustrated. Several variations in the muscles are also illustrated. The lumbosacral plexus and nerves of the leg in several specimens that show variations are illustrated.

Considerable individual variation was found in both the muscles and the nerves of the leg of the species studied. Certain muscles were more variable than others. Mm. flexor digitorum longus, obturator, caudofemoralis, and extensor hallucis longus showed the greatest number of variations. Mm. vastus medialis, femoritibialis internus, flexor perforatus digiti III, extensor brevis digiti III, and abductor digiti IV did not exhibit any variations considered significant. Certain legs showed a greater number of variations from the typical condition than did others.

Although most of the variations were minor, some were major. M. extensor proprius digiti III was present in two legs of *Pedioecetes* but absent in the other legs studied. A fleshy muscle slip connected M. caudofemoralis pars caudifemoralis with the tendinous raphe between Mm. flexor cruris lateralis and femorocruralis in two legs, whereas in others this connection was tendinous or even absent altogether. M. flexor cruris lateralis had an accessory slip arising from the caudal musculature in one leg. A vinculum connected the insertional tendons of Mm. flexor perforans et perforatus digiti II and flexor perforatus digiti II in one leg.

In most specimens there was as much variation between the muscles of the right and left legs of one individual as there was between individuals. The same was true for the nerves, except for the lumbosacral plexus, in which there was no significant variation between the right and left sides of any individual. The peroneal and obturator nerves varied less than the other nerves.

No constant differences in the muscles or nerves was found between *T. cupido pinnatus* and *T. c. attwateri.* One constant difference was found between *T. cupido* and *T. pallidicinctus:* the fleshy origin of M. extensor iliotibialis lateralis in *T. cupido* was thicker (associated with a thicker edge of the lateral iliac process).

Although no constant differences in the nerves were found between *Pedioecetes* and *Tympanuchus* (both species), 17 constant differences in the muscles were found between these two genera. Study of additional specimens possibly would show enough individual variation in some of these differences to reduce the number of constant differences to fewer than 17. Seven of these differences pertain to features of a single muscle—M. flexor cruris medialis. Some of the other differences are associated with the thinner and much less pronounced lateral iliac process in *Pedioecetes.* The picture of the differences between *Tympanuchus* and *Pedioecetes* that this study presents is radically different from that presented by the study of Hudson, *et al.* (1959).

The important differences in innervation between previous studies and the present one are discussed.

All of the muscles under consideration have been grouped as either dorsal or ventral muscles, according to their embryonic origin, as described by Romer (1927) and Wortham (1948). This grouping probably represents accurately the phylogenetic origin of these muscles. The dorsal muscles probably were originally supplied by dorsal nerves—the femoral and peroneal—and the ventral

muscles probably were originally supplied by ventral nerves—the obturator and tibial. This primitive muscle-nerve relationship has been relatively constant.

Several previous workers have reported some dorsal muscles supplied by ventral nerves and *vice versa*. Those findings should be viewed with suspicion until verified, because the proximal parts of the tibial and peroneal nerves are intimately associated and their relationship is easily misinterpreted. I found a branch of the tibial nerve that is closely associated with, and distributed with, the peroneal nerve. That branch of the tibial nerve has been mistakenly considered a part of the peroneal nerve by some workers. My study revealed no definite exceptions to the expected innervation.

Table 1. Synonymy of the Muscles of the Leg of Birds

Gadow (1891)	Hudson (1937)	Howell (1938)	Fisher & Goodman (1955)	Holmes
ilio-tibialis	ilio-tibialis	extensor iliotibialis lateralis	extensor ilio-tibialis lateralis	extensor iliotibialis lateralis
ilio-tibialis internus s. sartorius	sartorius	extensor iliotibialis anterior	extensor ilio-tibialis anterior	extensor iliotibialis anticus
ambiens	ambiens	ambiens	ambiens	ambiens
femori-tibialis externus	.....	.....	femoritibialis externus	vastus lateralis (a) pars postica (b) pars lateralis
femori-tibialis medius	femori-tibialis externus	vastus lateralis	vastus lateralis	
	femori-tibialis medius	vastus medialis	vastus medialis	vastus medialis
femori-tibialis internus	femori-tibialis internus		femoritibialis internus	femoritibialis internus
ilio-fibularis	biceps femoris	extensor iliofibularis	extensor ilio-fibularis	extensor iliofibularis
ilio-femoralis externus	glutaeus medius et minimus	piriformis	piriformis	piriformis
ilio-trochantericus posterior	ilio-trochantericus posterior	gluteus profundus	gluteus profundus	gluteus profundus

ilio–trochantericus anterior	ilio–trochantericus anterior	iliacus	iliacus	iliacus
ilio–trochantericus medius	ilio–trochantericus medius	.....	ilio–trochantericus medius	iliotrochantericus medius
ilio–femoralis internus	iliacus	psoas	psoas	psoas
caud–ilio–flexorius	semitendinosus	flexor cruris lateralis	flexor cruris lateralis (a) main head	flexor cruris lateralis
accessorius semitendinosi	accessorius semitendinosi	femorocruralis	(b) accessory heads	femorocruralis
ischio–flexorius	semimembranosus	flexor cruris medialis	flexor cruris medialis	flexor cruris medialis
caud–ilio–femoralis (a) pars caudi–femoralis	piriformis (a) pars caudi–femoralis	caudofemoralis	caudofemoralis (a) pars caudi–femoralis	caudofemoralis (a) pars caudifemoralis
(b) pars ilio–femoralis	(b) pars ilio–femoralis	flexor iliofemoralis	(b) pars ilio–femoralis	(b) pars iliofemoralis
ischio–femoralis	ischio–femoralis	flexor ischiofemoralis	flexor ischiofemoralis	flexor ischiofemoralis
pub–ischio–femoralis	adductor longus et brevis (a) pars anterior	adductor superficialis	adductor superficialis	adductor superficialis
	(b) pars posterior	adductor profundus	adductor profundus	adductor profundus

Table 1. Synonymy of the Muscles of the Leg of Birds—*Concluded*

Gadow (1891)	Hudson (1937)	Howell (1938)	Fisher & Goodman (1955)	Holmes
obturator	obturator internus	obturator	obturator internus	obturator
accessorii M. obturatoris	obturator externus		obturator externus	
gastrocnemius	gastrocnemius		gastrocnemius	gastrocnemius
flexor perforans et perforatus digiti II	flexor perforans et perforatus digiti II		flexor perforans et perforatus digiti II	flexor perforans et perforatus digiti II
flexor perforans et perforatus digiti III	flexor perforans et perforatus digiti III		flexor perforans et perforatus digiti III	flexor perforans et perforatus digiti III
flexor perforatus digiti IV	flexor perforatus digiti IV		flexor perforatus digiti IV	flexor perforatus digiti IV
flexor perforatus digiti III	flexor perforatus digiti III		flexor perforatus digiti III	flexor perforatus digiti III
flexor perforatus digiti II	flexor perforatus digiti II		flexor perforatus digiti II	flexor perforatus digiti II
flexor hallucis longus	flexor hallucis longus		flexor hallucis longus	flexor hallucis longus
plantaris	plantaris		plantaris	plantaris
flexor profundus s. perforans	flexor digitorum longus		flexor digitorum longus	flexor digitorum longus

popliteus	popliteus		popliteus	popliteus
peroneus superficialis	peronaeus longus		peroneus longus	peroneus longus
tibialis anticus	tibialis anterior		tibialis anterior	tibialis anticus
extensor digitorum communis	extensor digitorum longus		extensor digitorum longus	extensor digitorum longus
peroneus profundus	peronaeus brevis		peroneus brevis	peroneus brevis
extensor hallucis brevis	extensor hallucis longus		extensor hallucis longus	extensor hallucis longus
abductor digiti II	abductor digiti II		abductor digiti II	abductor digiti II
extensor brevis digiti III	extensor proprius digiti III		extensor brevis digiti III	extensor brevis digiti III
extensor proprius digiti III			extensor proprius digiti III	extensor proprius digiti III
extensor brevis digiti IV	extensor brevis digiti IV		extensor brevis digiti IV	extensor brevis digiti IV
flexor brevis digiti III	lumbricalis		.....	lumbricalis
abductor digiti IV	abductor digiti IV		abductor digiti IV	abductor digiti IV
flexor hallucis brevis	flexor hallucis brevis		flexor hallucis brevis	flexor hallucis brevis
adductor digiti II	adductor digiti II		adductor digiti II	.....
adductor digiti IV	adductor digiti IV		.....	.....

Table 2. Relative Sizes (in Percentages) of Some Muscles in Tympanuchus and Pedioecetes

Muscle	*Tympanuchus*			*Pedioecetes*		
	Ave.	Range	No.[1]	Ave.	Range	No.[1]
Iliacus: width of fleshy origin (divided by length of ilium)	.10	.08–.11	13	.19	.17–.19	6
Flexor cruris lateralis: maximum width of exposed part (divided by length of ilium)	.22	.19–.27	13	.31	.27–.36	6
Flexor cruris medialis: width of origin (divided by length of ilium)	.11	.08–.16	13	.22	.19–.23	6
Flexor cruris medialis: width of insertion (divided by length of tibiotarsus)	.09	.08–.13	13	.17	.15–.17	4
Adductor superficialis: width of origin (divided by length of ilium)	.20	.17–.23	13	.13	.10–.16	5
Femorocruralis: distance of proximal end of origin from proximal end of femur (divided by length of femur)	.59	.55–.63	13	.40	.38–.43	6
Extensor digitorum longus: length of fleshy belly (divided by length of tibiotarsus)	.73	.64–.83	13	.59	.50–.62	4

1. No. = number of legs.

TABLE 3. OCCURRENCE OF INDIVIDUAL VARIATIONS IN MUSCLES

	T.p.								T.c.p.						T.c.a.			P.p.					
	1 L	1 R	2 L	2 R	3 L	3 R	4 L	5 R	1 L	1 R	2 L	2 R	3 L	4 L	1 L	1 R	2 L	1 L	1 R	2 L	3 L	3 R	4 L
Ambiens																							
origin partly fleshy																x							
Vastus lateralis																							
no vincula												x		x									
Extensor iliofibularis																							
insertional tendon double										x													
Piriformis																							
posteroproximal corner tendinous		x									x				x	x		x					
insertion fused to flexor ischiofemoralis												x											
Iliotrochantericus medius																							
not notched					x	x									x								
anterior part with fleshy origin														x				x		x			x
insertion fused to gluteus profundus																x							
muscle split																		x					
Flexor cruris lateralis																							
accessory slip present												x											
Flexor cruris medialis																							
origin from pubis													x			x							
insertion partly fleshy																			x	x		x	x
insertional tendon split																			x				
Caudofemoralis																							
accessory slip fleshy			x	x																			
tendinous area in belly of pars caudifemoralis									x	x				x									
origin from pubis										x													
insertion entirely tendinous																						x	

Table 3. Occurrence of Individual Variations in Muscles—*Concluded*

	T.p.								T.c.p.						T.c.a.			P.p.					
	1 L	1 R	2 L	2 R	3 L	3 R	4 L	5 R	1 L	1 R	2 L	2 R	3 L	4 L	1 L	1 R	2 L	1 L	1 R	2 L	3 L	3 R	4 L
Flexor ischiofemoralis																							
insertion partly fleshy	x						x													x			
Adductor superficialis																							
groove for flexor cruris medialis present			x	x		x		x															
completely fused with adductor profundus																			x				
Adductor profundus																							
proximal part of insertion tendinous																x							
distal end of insertion tendinous												x											
Obturator																							
independent slip of pars antica present				x						x													
slip of pars antica fused to pars postica							x														x		
independent slip of pars dorsalis present								x							x	x			x				
pars dorsalis fused with pars antica																		x					
Gastrocnemius																							
pars interna overlaps peroneus longus															x								
Flexor perforans et perforatus digiti II																							
anterior head entirely tendinous								x															
vinculum joins flexor perforatus digiti II	x																						
origin from superficial surface of patellar tendon													x										
Flexor perforans et perforatus digiti III																							
accessory head present					x	x																	
Flexor perforatus digiti II																							
roof of hypotarsal canal bony									x												x	x	

Plantaris																							
accessory head present					x																		
origin from medial collateral ligament																	x						
Flexor digitorum longus																							
notched for peroneal nerve			x	x			x	x														x	
origin from tendon of extensor iliofibularis						x																	
third dorsal slip present in digit IV			x	x											x	x	x		x	x	x	x	
third dorsal slip present in digit III			x	x	x								x	x	x	x	x	x	x			x	x
second dorsal slip present in digit II			x	x	x							x		x	x	x	x	x	x			x	x
vinculum joins flexor perforatus digiti IV																				x	x	x	x
Peroneus longus																							
origin from patellar tendon	x	x			x	x																	x
Tibialis anticus																							
accessory insertion absent							x															x	
Extensor digitorum longus																							
lateral branch of tendon not ossified	x				x	x		x										x	x	x	x	x	x
origin from posterior surface of outer cnemial crest																		x		x			x
Extensor hallucis longus																							
origin lateral to retinaculum		x																x					
distal fibers of distal head insert independently					x													x	x		x		x
accessory bundle present															x								
entire distal head inserts independently																				x			
Abductor digiti II																							
accessory insertion present													x										
Extensor proprius digiti III																							
present																		x					x

Table 4. Number of Muscular Variations in Common Between the Legs Studied

Leg	Other leg of same specimen	T.p.								T.c.p.						T.c.a.			P.p.						No other legs
		1 L	1 R	2 L	2 R	3 L	3 R	4 L	5 R	1 L	1 R	2 L	2 R	3 L	4 L	1 L	1 R	2 L	1 L	1 R	2 L	3 L	3 R	4 L	
T.p. 1L	1	–	–			2	2	1	1										1	1	2	1	1	2	1
T.p. 2R	6			–	–	2	1	1	2		1		1	1	2	3	3	3	2	3	1	1	4	2	0
T.p. 3L	4	2	1	2	2	–	–		1				1	1	2	3	2	2	4	4	1	2	3	5	1
T.c.p. 1R	1				1					–	–				1										2
T.c.p. 2R	0			1	1	1						–	–		2	1	1	1	1	1			1	1	3
T.c.a. 1R	5		1	3	3	2			1			1	1	2	2	–	–	3	3	4	1	1	3	2	3
P.p. 1L	4		2	2	2	3						1	1	1	3	3	3	2	–	–	3	2	3	7	2
P.p. 3R	4			4	4	2		2	1	1			1	1	2	3	3	3	3	5	4	–	–	5	1

TABLE 5. OCCURRENCE OF INDIVIDUAL VARIATIONS IN NERVES

	T.p.								T.c.p.						T.c.a.			P.p.					
	1 L	1 R	2 L	2 R	3 L	3 R	4 L	5 R	1 L	1 R	2 L	2 R	3 L	4 L	1 L	1 R	2 L	1 L	1 R	2 L	3 L	3 R	4 L
Lumbosacral plexus																							
two furcal nerves			x	x											x	x					x	x	x
S9 with three branches								x															
prefixed													x		x	x	x			x	x	x	x
sciatic nerve with six roots			x	x									x		x	x	x			x	x	x	x
obturator nerve from S2 and S3 only																	x				x	x	x
femoral nerve mainly from S2–S4													x		x	x	x			x	x	x	x
Femoral nerve																							
anterior division innervates extensor iliotibialis lateralis							x	x		x	x		x										
dorsal division fused with anterior division	x																		x		x		x
dorsal division fused with middle division			x	x		x									x					x	x		
two branches to iliacus			x																		x		
middle division anastomoses with anterior division			x	x										x	x	x							
anterodorsal division does not go through femoral notch					x	x																	
branch of anterior division perforates iliacus																x							
cutaneous branch perforates extensor iliotibialis lateralis											x	x											
branch of middle division perforates vastus medialis														x									

Table 5. Occurrence of Individual Variations in Nerves—*Concluded*

	T.p.								T.c.p.						T.c.a.			P.p.					
	1 L	1 R	2 L	2 R	3 L	3 R	4 L	5 R	1 L	1 R	2 L	2 R	3 L	4 L	1 L	1 R	2 L	1 L	1 R	2 L	3 L	3 R	4 L
branch to vasti innervates extensor iliotibialis lateralis											x												
anterior branch of anterior division cutaneous																		x	x				x
Sciatic nerve																							
twig to pars caudifemoralis independent			x																				
branch to flexor cruris lateralis does not perforate caudofemoralis	x	x		x					x	x	x	x	x				x						
paraperoneal nerve enters peroneal sheath	x		x	x			x											x	x				
cutaneous peroneal branch perforates gastrocnemius pars externa							x																
cutaneous peroneal branch absent			x	x				x															
distal cutaneous tibial branch absent								x															
twig to tail present			x			x		x								x	x		x			x	
nonmuscular peroneal twig deep to vastus lateralis pars postica			x	x				x									x						
branch to flexor cruris medialis from posterior tibial division													x					x	x				
extra twigs join cutaneous tibial branches													x										
branch to flexor cruris medialis an independent division																				x	x	x	

branch to flexor cruris medialis perforates flexor ischiofemoralis																			x				
two twigs to flexor ischiofemoralis																			x	x	x	x	x
independent extra branch innervates extensor iliofibularis																					x		
branch to femorocruralis innervates gastrocnemius pars media																						x	
Peroneal nerve																							
superficial and deep peroneal nerves do not join	x				x		x	x															
Tibial nerve																							
independent extra branch innervates flexor perforatus digiti IV					x	x																	
anastomosis involving posterior division					x	x																	
branch to gastrocnemius pars externa an independent division						x																	
branch to gastrocnemius pars media innervates femorocruralis	x					x																	
extra branch innervates flexor perforatus digiti III																x							
branch to gastrocnemius pars interna perforates plantaris															x								
branch to gastrocnemius pars interna innervates plantaris																					x		

Table 6. Number of Nerve Variations in Common Between the Legs Studied

Leg	Other leg of same specimen	T.p.								T.c.p.						T.c.a.			P.p.						No other legs
		1 L	1 R	2 L	2 R	3 L	3 R	4 L	5 R	1 L	1 R	2 L	2 R	3 L	4 L	1 L	1 R	2 L	1 L	1 R	2 L	3 L	3 R	4 L	
T.p. 1L	1	–	–	1	2	1	1	2	1	1	1	1	1	1				1	1	2		1		1	0
T.p. 2L	5	1		–	–		2	1	3						1	2	2	2	1	2	1	2	1		1
T.p. 3R	3	1		2	1	–	–		1							1	1	1		1	1	1	1		1
T.c p. 1R	1	1	1		1			1	1	–	–	2	1	2				1							0
T.c.p. 2L	2	1	1		1			1	1	1	2	–	–	2				1							1
T.c.a. 1R	1			2	1		1		1						1	–	–	1		1			1		2
P.p. 1R	3	2		2	1		1	1	1					1			1	1	–	–	1	2	2	3	1
P.p. 3L	2	1		2	1		1									1				2	3	–	–	2	2

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18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baimoys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690

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*6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

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Vol. 12. 1. Functional morphology of three bats: Sumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
*2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
*4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.
9. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pediocecetes). By E. Bruce Holmes. Pp. 363-474, 20 figs. October 25, 1963.

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A New Genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas

BY

JOAN ECHOLS

University of Kansas
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A New Genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas

BY

JOAN ECHOLS

INTRODUCTION

In 1931 and 1932, H. H. Lane, C. W. Hibbard and W. K. McNown collected the specimens that Hibbard (1933) described and made the basis of two new species. These were from the Rock Lake shale member of the Stanton formation, six miles northwest of Garnett, Anderson County, Kansas. In 1954, from a locality (KAn-1/D, see page 480) approximately one fourth mile southwest of the first locality, specimens were quarried by F. E. Peabody, R. W. Wilson and R. Weeks. In 1955 R. R. Camp collected additional blocks of Rock Lake shale from this second locality. Study of all of the materials from the above mentioned localities reveals the existence of an hitherto unrecognized genus of coelacanth. It is named and described below.

I wish to thank Prof. Theodore H. Eaton, Jr., for suggesting the project and for much helpful advice. I am indebted to Dr. E. I. White of the British Museum (Natural History) for furnishing a cast of the endocranium of *Rhabdoderma elegans* (Newberry) for comparison, and to Drs. Donald Baird (Princeton University), Bobb Schaeffer (American Museum of Natural History) and R. H. Denison (Chicago Natural History Museum) for loans and exchanges of specimens for comparison. I am grateful to Dr. Bobb Schaeffer for advice on the manuscript. Mr. Merton C. Bowman assisted with the illustrations. The study here reported on was made while I was a Research Assistant supported by National Science Foundation Grant G-14013.

SYSTEMATIC DESCRIPTIONS

Subclass CROSSOPTERYGII

Superorder COELACANTHI

Order Coelacanthiformes

Suborder DIPLOCERCIDOIDEI

Family DIPLOCERCIDAE

Subfamily Rhabdodermatinae, new subfamily

Type genus.—*Rhabdoderma* Reis, 1888, Paleontographica, vol. 35, p. 71.

Referred genus.—*Synaptotylus* new, described below.

Horizon.—Carboniferous.

Diagnosis.—Sphenethmoid region partly ossified, and consisting of basisphenoid, parasphenoid, and ethmoid ossifications; paired basipterygoid process and paired antotic process on basisphenoid; parasphenoid of normal size, and closely associated with, or fused to, basisphenoid; ethmoids paired in *Rhabdoderma* (unknown in *Synaptotylus*).

Discussion.—Because of the great differences in endocranial structure between the Devonian and Pennsylvanian coelacanths, they are here placed in new subfamilies. The two proposed subfamilies of the family Diplocercidae are the Diplocercinae and the Rhabdodermatinae. The Diplocercinae include those coelacanths having two large unpaired bones in the endocranium (at present this includes *Diplocercides* Stensiö, *Nesides* Stensiö and *Euporosteus* Jaekel). The subfamily Rhabdodermatinae is composed of coelacanths having reduced endocranial ossification, as described in detail above, and now including *Rhabdoderma* Reis and *Synaptotylus* n. g.

Members of this subfamily differ from those of the subfamily Diplocercinae in having several paired and unpaired elements in the sphenethmoid region of the endocranium, instead of only one larger ossification. They differ from those of the suborder Coelacanthoidei in the retention of basipterygoid processes.

Synaptotylus is more closely related to *Rhabdoderma* than to the Diplocercines because the anterior portion of the endocranium contains only a basisphenoid, parasphenoid, and probably ethmoids. The sphenethmoid region was certainly not a large, unpaired unit as in the Diplocercines. Probably the posterior part, the otico-occipital region (not known in *Synaptotylus*), was much more nearly like that of *Rhabdoderma*, which consisted of unpaired basi-occipital and supraoccipital, and paired prootics, exoccipitals, and anterior and posterior occipital ossifications (Moy-Thomas, 1937:

figs. 3, 4). Moy-Thomas (1937:389) points out that in *Rhabdoderma* the occipital region is "considerably more ossified" than in any coelacanths other than the Devonian forms. Berg (1940:390) thought that the Carboniferous coelacanths should be placed in a separate family because they did not have two large, unpaired bones in the endocranium. *Rhabdoderma* and *Synaptotylus* represent another stage in evolution of the endocranium in coelacanths, and, if classification is to be based on endocranial structure, then this stage (represented by the two genera) may later be given family rank as Berg suggested. Because *Rhabdoderma* and *Synaptotylus* have only part of the sphenethmoid region ossified and because they retain basipterygoid processes, they are considered to be related and are included in the subfamily Rhabdodermatinae.

Synaptotylus, new genus

Type species.—*Synaptotylus newelli* (Hibbard).

Horizon.—Rock Lake shale member, Stanton formation, Lansing group, Missouri series, Upper Pennsylvanian.

Diagnosis.—Late Pennsylvanian fishes of small size, having the following combination of characters: on basisphenoid, knoblike antotic processes connected by a low ridge to basipterygoid processes; entire ventral surface of parasphenoid toothed; anterior margin of parasphenoid notched and no evidence of hypophyseal opening. Dermal bones of skull smooth or with low, rounded tubercles and striae; fronto-ethmoid shield incompletely known but having one pair of large rectangular frontals with posterolaterally slanting anterior margins; intertemporals large, the lateral margins curving laterally; postorbital triangular, apex downward; subopercular somewhat triangular; squamosal carrying sensory canal that curves down posteriorly and extends onto a ventral projection; opercular generally triangular; supratemporals elongate, curving to fit lateral margin of intertemporals; circumorbital plates lightly ossified. Palatoquadrate complex consisting of endopterygoid and ectopterygoid (both toothed on medial surface), quadrate, and metapterygoid, the latter smooth and having widened border for articulation on anterodorsal margin. Pectoral girdle consisting of cleithrum and clavicle (supracleithrum not seen); small projection on medial surface of posterior portion of cleithrum; horizontal medial process on clavicle. Pelvic plate bearing three anteriorly diverging apophyses, and one denticulate ventromedian process for articulation to opposite plate. Lepidotrichia jointed distally,

but not tuberculated. Scales oval, having posteriorly converging ridges on posterior exposed parts.

The name refers to the most distinctive character of the genus, the connected antotic and basipterygoid processes on the basisphenoid, and is derived from Greek, *synaptos*—joined, *tylos* (masc.)—knob, projection.

Synaptotylus is excluded from the advanced suborder Coelacanthoidei by the retention of basipterygoid processes on the basisphenoid. *Synaptotylus* differs from *Rhabdoderma* in several characters of the basisphenoid, the most important being: knoblike antotic processes (those of *Rhabdoderma* are wider, more flattened and more dorsal in position); small, lateral basipterygoid processes (in *Rhabdoderma* these are larger and farther ventral in position).

Synaptotylus newelli (Hibbard)

Coelacanthus newelli Hibbard, 1933, Univ. Kansas Sci. Bull., 21:280, pl. 27, figs. 2, 3.

Coelacanthus arcuatus Hibbard, 1933, Univ. Kansas Sci. Bull., 21:282, pl. 26, fig. 8; pl. 27, fig. 1.

Rhabdoderma elegans Moy-Thomas, 1937 (in part), Proc. Zool. Soc. London, 107(ser. B, pt. 3):399.

Type.—K. U. no. 786F.

Diagnosis.—Same as for the genus.

Horizon.—Rock Lake shale member, Stanton formation, Lansing group, Missouri series, Upper Pennsylvanian.

Localities.—The specimens studied by Hibbard (K. U. nos. 786F, 787F, 788) and no. 11457 were taken from the Bradford Chandler farm, from the original quarry in SW¼, SE¼, sec. 32, T.19S, R.19E. The remainder were collected from University of Kansas Museum of Natural History locality KAn-1/D, a quarry in sec. 5, T.19S, R.19E. Both of these are approximately six miles northwest of Garnett, Anderson County, Kansas.

Referred specimens.—K. U. nos. 786F, 787F, 788, 9939, 11424, 11425, 11426, 11427, 11428, 11429, 11430, 11431, 11432, 11433, 11434, 11449, 11450, 11451, 11452, 11453, 11454, 11455, 11457.

Preservation.—Preservation of many of the specimens is good, few are weathered, but most of the remains are fragmentary and dissociated. One specimen (the type, no. 786F) and half of another were nearly complete. Specimens are found scattered throughout the Rock Lake shale (see p. 498).

Morphology.—Terminology used for bones of the skull is that of Moy-Thomas (1937) and Schaeffer (1952).

Endocranium and parasphenoid

The basisphenoid (see fig. 1) has been observed in only one specimen (K. U. no. 9939) in posterodorsal and ventral views. The basisphenoid, although somewhat crushed, appears to be fused to the parasphenoid. Both antotic and basipterygoid processes are

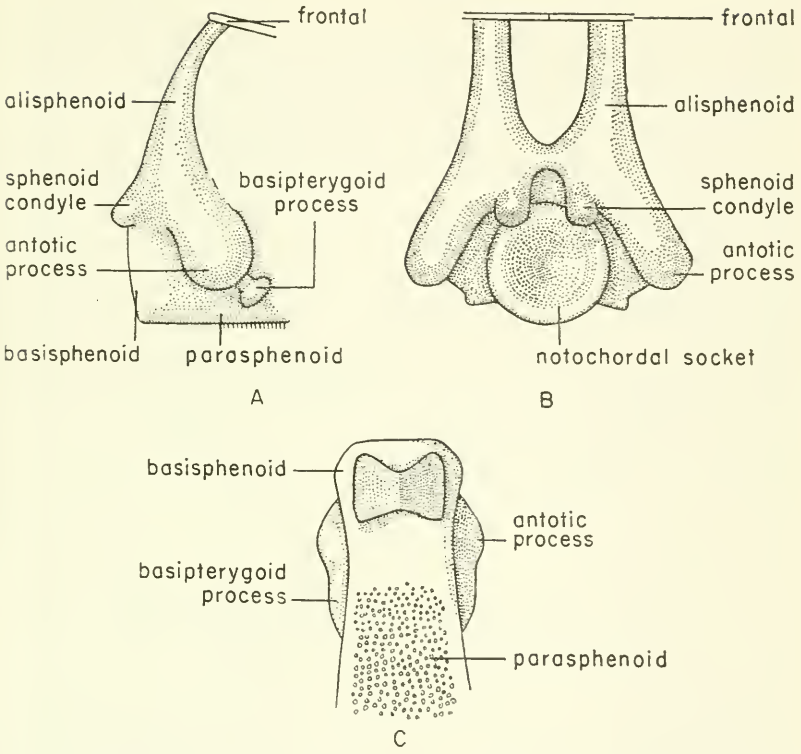

Fig. 1. *Synaptotylus newelli* (Hibbard). Restoration of the basisphenoid, based on K. U. no. 9939, × 5. A, lateral view, B, posterior view, C, ventral view.

present, and are connected by a low, rounded ridge. The antotic processes are large, bulbar projections. These processes in *Rhabdoderma* are wider and more flattened (Moy-Thomas, 1937:figs. 3, 4). The antotic processes are at mid-point on the lateral surface, not dorsal as in *Rhabdoderma*, and both the processes and the ridge are directed anteroventrally. The basipterygoid processes are smaller, somewhat vertically elongated projections, situated at the end of the low connecting ridge extending anteroventrally from the antotic processes, and are not basal as are those of *Rhabdoderma*. The sphenoid condyles, seen in posterior view, issue from the dorsal margin of the notochordal socket. The margins of the socket are rounded, and slope down evenly to the center. A slight depression situated between and dorsal to the sphenoid condyles is supposedly for the attachment of the intercranial ligament (Schaeffer and Gregory, 1961:fig. 1). The alisphenoids extend

upward, anterodorsally from the region above the sphenoid condyles, and may connect to ridges on the ventral surface of the frontals. The lateral laminae are not preserved, and their extent is unknown.

In viewing the changes in the endocranium of Carboniferous and Permian coelacanths, it would be well to consider the mechanical relationship of the loss of the basipterygoid processes to the effect on swallowing prey. Evidently many of the coelacanths, *Latimeria* for example, are predators (Smith, 1939:104); to such fishes a more efficient catching and swallowing mechanism would be an adaptive improvement. Stensiö (1932:fig. 14) presents a cross section of the ethmosphenoid moiety of the endocranium of *Diplocercides kayseri* (von Koenen) showing the metapterygoid of the palatoquadrate loosely articulated to both the antotic and basipterygoid processes. According to Tchernavin (1948:137) and Schaeffer and Rosen (1961:190) the swallowing of large prey depends on the ability of the fish to expand its oral cavity by allowing the posteroventral portion of the palatoquadrate and the posterior end of the mandible to swing outward. Where the palatoquadrate articulates with the basisphenoid at the antotic and basipterygoid processes, as in the Devonian coelacanths, it can not swing so far laterally as where it articulates with only the dorsal, antotic process. Perhaps the loss of the basipterygoid articulation reflects the development of a more efficient mechanism for swallowing prey in these fishes. Schaeffer and Rosen (1961:191, 193) show that in the evolution of the actinopterygians several changes improved the feeding mechanism: some of these changes are: (1) freeing of the maxilla from the cheek, giving a larger chamber for the action of the adductor mandibulae; (2) development of a coronoid process on the mandible; and (3) increase in torque around the jaw articulation. In coelacanths, at least some comparable changes occurred, such as: (1) loss of the maxillary, thus increasing the size of the adductor chamber; (2) development of the coronoid bone, affording a greater area for muscle attachment; (3) development of an arched dorsal margin on the angular; (4) modification of the palatoquadrate complex, with resultant loss of the basipterygoid processes. In *Synaptotylus* the basipterygoid processes are small, not basally located, and perhaps not functional. A more efficient feeding mechanism developed rapidly during the Carboniferous and has remained almost unaltered.

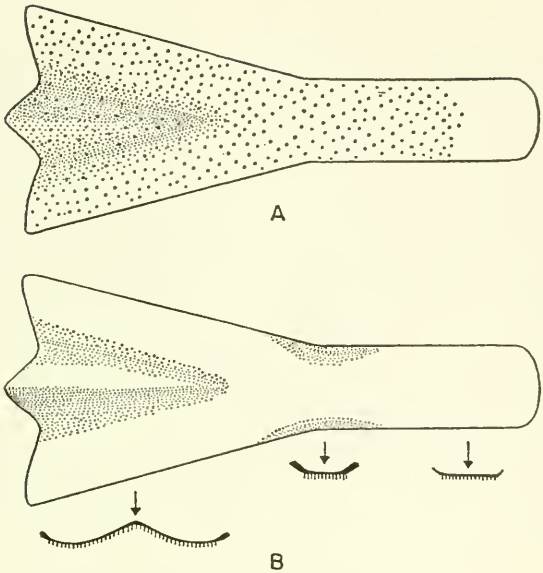

Fig. 2. *Synaptotylus newelli* (Hibbard). Restoration of the parasphenoid, based on K. U. nos. 9939, 11451, × 5. A, ventral view, B, dorsal view and cross sections.

The parasphenoid (see fig. 2) is a shovel-shaped bone having a wide anterior portion and a narrower posterior portion of nearly uniform width. Most of the ventral surface is covered with minute granular teeth. The anterior margin is flared and curved posteromedially from the lateral margin to a median triangular projection. The lateral margins curve smoothly from the greatest anterior width to the narrow central portion, where the margins become somewhat thickened and turned dorsally. Posterior to this the lateral margins are probably nearly straight. The external surface of the anterior section is nearly flat and has a central depressed area the sides of which slope evenly to the center. The internal surface is smooth and centrally convex. Because of the fragmentary nature of all four observed specimens, total length was not measured but is estimated to be 15 to 20 mm. The opening of the hypophyseal canal was not present, possibly because of crushing. Ethmoidal ossifications were not preserved in any of the specimens studied. The parasphenoid differs from that of *Rhabdoderma elegans* (Newberry) in being more flared and widened anteriorly and more concave centrally.

Dermal bones of the skull

Various portions of the cranial roof are preserved in several specimens (see fig. 3). For comparisons with *Rhabdoderma elegans,* see Moy-Thomas (1937:fig. 1).

The premaxillaries and rostral elements are not preserved in any of the specimens. Only one pair of relatively large frontals have been observed; they are 5.5 to 9.0 mm. long and 2.0 to 3.5 mm. wide. These are nearly flat bones, with the greatest width posteriorly 0.1 to 1.0 mm. wider than the anterior portion. The midline suture is straight, the lateral margins are nearly straight, the anterior margin slopes evenly posterolaterally, and the posterior margin is slightly convex to straight. The anterior margin in *R. elegans* is essentially straight. Ornamentation consists of sparse, unevenly spaced, coarse tubercles or short striae. In one specimen both bones have small clusters of tubercles near the lateral margins and about 2.0 mm. from the posterior margin. None of these bones has alisphenoids or ridges on the ventral surface, as Stensiö (1921:65, 97) described for *Wimania* and *Axelia.*

Only six supraorbitals have been preserved (see fig. 3). These are nearly square, flat, thin bones lying nearly in place adjacent to

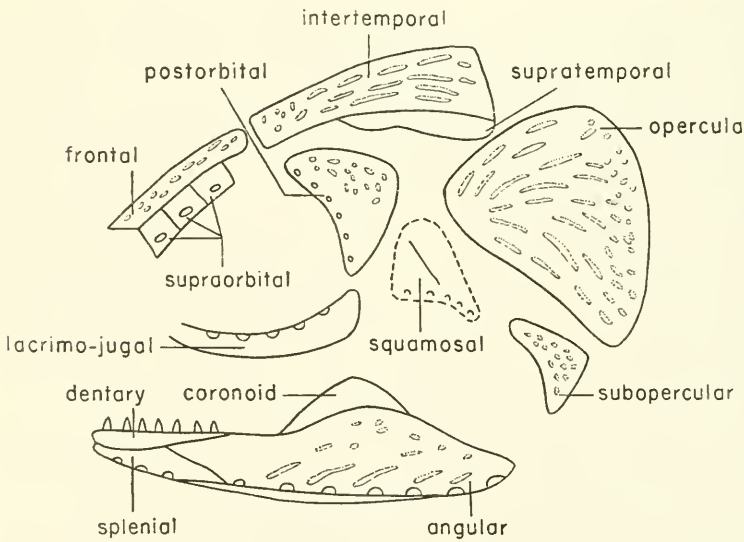

FIG. 3. *Synaptotylus newelli* (Hibbard). Diagram of the dermal bones of the skull, in lateral view, based on K. U. nos. 788 and 11432. × 2½ approximately.

a frontal on K. U. no. 788. The smallest is anterior; the margins of all are nearly straight. The bones are unornamented. Each bears a pore of the supraorbital line just below the midline. The supraorbitals of *R. elegans* have a triangular outline and do not bear pores.

Intertemporals (fig. 3) on several specimens vary from approximately 9.0 to 15.0 mm. in length, 2.0 to 2.7 mm. in anterior width, and increase to 4.5 to 8.0 mm. in maximum posterior width. The midline suture is straight, the anterior margin is concave and the lateral margin proceeds laterally in a concave curve to the widest portion. In *R. elegans* only the anterior half of the corresponding margin is concave. The posterior margin is slightly rounded and slopes anteriorly toward the lateral margin. Ornamentation is usually of randomly oriented tubercles and striae, although striae are more common in the posterior third and may be longitudinal, whereas tubercles occur mainly on the anterior section. No evidence of sensory pores, as seen on the intertemporal of *R. elegans*, has been found.

The supratemporals were observed on only one specimen (K. U. no. 788), (fig. 3). Sutures were difficult to distinguish but the medial margin is presumed to curve to fit and to articulate with the lateral margins of the intertemporals. Lateral margins are smoothly curved but the anterior and posterior margins were broken off. There appears to be no ornamentation on this bone. The supratemporals are much more elongated and curving than those in *R. elegans*.

The cheek region is nearly complete in one specimen (K. U. no. 788), and scattered parts occur in a few others (see fig. 3). The lacrimojugal of no. 788 is elongate, with both ends curving dorsally. It differs from the lacrimojugal in *R. elegans*, in which the anterior end extends anteriorly and is not curved dorsally. The posterior and anterior margins are not preserved; the greatest height appears to be posterior. Pores of the suborbital portion of the infraorbital sensory canal are seen on the dorsal surface of the bone. In *R. elegans* the pores are on the lateral surface. A section of the lacrimojugal on specimen no. 11425, broken at both ends, shows a thin layer of bone perforated by the pores and covering a groove for the canal within the dorsal margin of the bone. Both specimens are unornamented.

A nearly complete postorbital (fig. 3) on specimen no. 788 is nearly triangular, with the apex ventral. The concave anterior

margin bears pores of the postorbital part of the infraorbital line. Ornamentation consists of widely spaced, coarse tubercles.

Part of one squamosal is preserved. It is somewhat triangular and its apex is ventral. This bone is associated with the postorbital, subopercular and lacrimojugal on no. 788. The preopercular sensory line passes down the curving ventral margin of this bone, and extends ventrally onto a narrow projection. A low ridge, nearly vertical, passes dorsally from about midpoint of the canal to the dorsal portion. The anterior margin is nearly straight, the ventral margin is concave, and the dorsal margin is convex dorsally but may be incomplete. Perhaps the squamosal and preopercular are fused. The surface appears smooth; the view may be of the medial side. The squamosal of *R. elegans* is nearly triangular and notably different from that of *Synaptotylus newelli.*

The subopercular (fig. 3) shows closely spaced tubercles on the lateral surface. The bone is an elongated, irregular triangle with the apex pointing anterodorsally. The margins are incomplete, except for the concave, curving anterior margin.

Numerous operculars (fig. 3) occur in the suite of specimens, both isolated and nearly in place. Each is subtriangular; the apex of the triangle is ventral. A slight convexity projects from the anterodorsal border. The posterior margin is broadly but shallowly indented. Otherwise the margins are smooth. Maximum height ranges from 8.0 to 11.0 mm., and maximum width from 8.0 to 13.0 mm. Ornamentation varies from a few widely spaced, randomly oriented tubercles to closely spaced tubercles merging posteriorly into striae. On some specimens these are parallel to the dorsal border, and oblique in the central portion. On the posterior margins of several operculars the striae break up into tubercles. A few operculars have closely spaced tubercles over much of the surface. The internal surface is smooth.

Visceral skeleton

The palatoquadrate complex, best seen on K. U. no. 9939 (fig. 4), consists of endopterygoid, ectopterygoid, metapterygoid and quadrate. No trace of epipterygoids, dermopalatines or autopalatines, such as Moy-Thomas (1937:392, fig. 5) described for *Rhabdoderma,* has been observed.

The endopterygoid has a long, ventral, anteriorly-directed process, and an anterodorsal process that meets the metapterygoid in forming the processus ascendens. The suture between the endoptery-

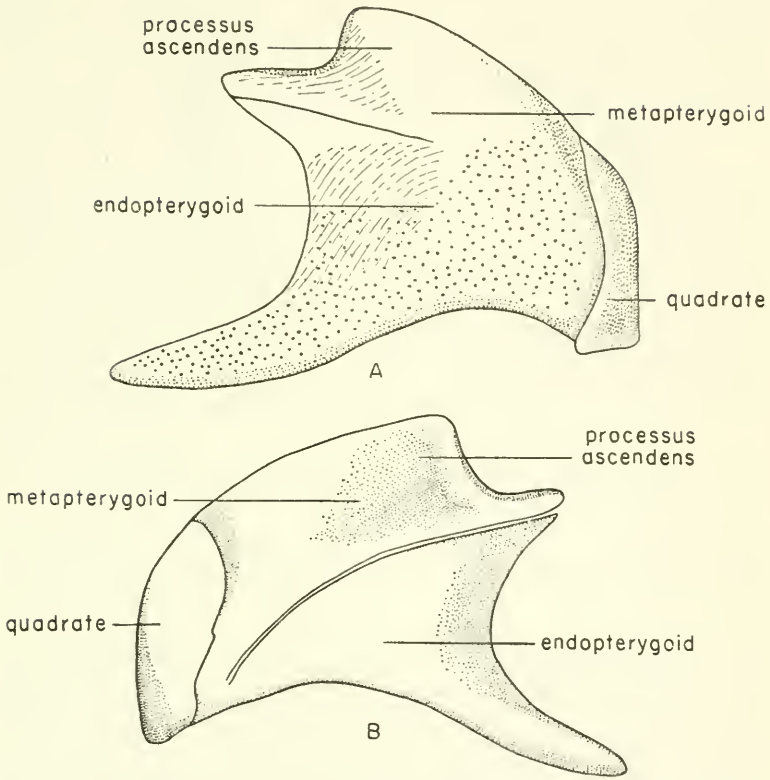

Fig. 4. *Synaptotylus newelli* (Hibbard). Restoration of the palatoquadrate complex, based on K. U. no. 9939, × 5. A, medial view, B, lateral view.

goid and metapterygoid, seen in lateral view, is distinct in some specimens and has an associated ridge; these bones appear to be fused in others, without regard to size. This suture curves dorsally from a point anterior to the quadrate and passes anterodorsally to the extremity of the processus ascendens. The suture is visible on the medial side only near the processus ascendens, for it is covered by a dorsal, toothed extension of the endopterygoid. The endopterygoid has a smooth lateral surface; the medial surface is covered with tiny granular teeth, in characteristic "line and dot" arrangement. The teeth extend onto the ventral surface of the ventral process.

Two long, narrow, splintlike bones covered on one surface with granular teeth are interpreted as ectopterygoids. These are 13.0 and 16.0 mm. long and each is 1.5 mm. wide. Orientation of these is unknown, but they probably fitted against the ventral surface

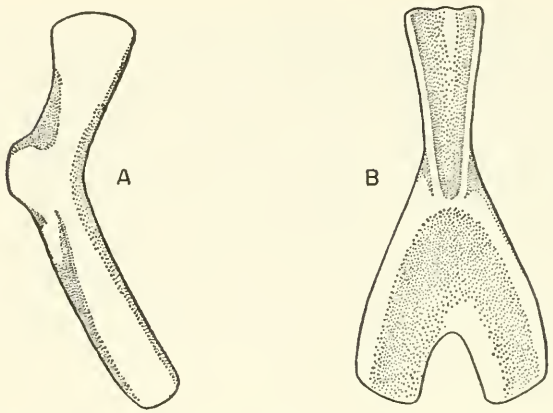

FIG. 5. *Synaptotylus newelli* (Hibbard). A, ceratohyal, lateral (?) view, based on K. U. nos. 11429 and 11457, × 5. B, urohyal, based on K. U. no. 11457, × 5.

of the ventral process of the endopterygoid (Moy-Thomas, 1937: fig. 5).

The metapterygoid has a smooth surface in both views. The dorsal edge has a thickened, flared margin that presumably articulated with the antotic process of the basisphenoid. No articular surface for the basipterygoid process has been observed.

The quadrate is distinct and closely applied to the posteroventral margin of the complex. In medial view the margin is nearly straight and continues to the ventral edge. The ventral surface is thickened and forms a rounded, knoblike articular surface. In lateral view the surface is smooth; the anterior margin is irregular (or perhaps broken on all specimens), and proceeds in an irregular convex curve from the posterior to the ventral margin.

The general shape of the palatoquadrate complex is most nearly like that of *Rhabdoderma elegans* (Moy-Thomas, 1937:fig. 5). The orientation of the complex in the living fish was probably oblique, with the processus ascendens nearly vertical, the quadrate oblique, and the ventral process of the endopterygoid extending dorsoanteriorly and articulating with the parasphenoid.

Of the hyoid arch only the ceratohyals (see fig. 5A) are preserved in several specimens. These are long, curved bones with a posteroventral process and widened, flaring posterior margin. The medial (?) surface is concave in one specimen. The lateral (?) surface displays a distinct ridge on several specimens, arising on the dorsal

surface opposite the posteroventral process and extending diagonally to the anteroventral end of the anterior limb. The impression of one other specimen appears to have a central ridge because of greater dorsal thickness and narrowness. Both surfaces are unornamented.

The urohyal (see fig. 5B) is an unornamented, Y-shaped bone, with the stem of the Y pointing anteriorly. Orientation with respect to dorsal and ventral surfaces is uncertain. In one view a faint ridge, also Y-shaped, occurs on the expanded posterior portion, and the surface is convex. The anterior process has a convex surface, sloping evenly off to the lateral margin; the opposite side of the process has a concave surface. The posterior portion has a slightly depressed area (see fig. 5B) at the junction of the "arms" of the Y.

The five branchial arches are represented by the ceratobranchials, several of which are preserved on K. U. no. 11431. These are long bones with anteriorly curving ventral ends. The medial surfaces are partly covered with minute granular teeth; only the dorsal part is without teeth. The dorsal articular surface is convex dorsally and rounded.

The mandible (fig. 3), the best specimens of which are K. U. nos. 788 and 11425, is seen only in lateral and ventral views, with only angular, splenial and dentary visible.

The angular forms the main body of the mandible, and is similar to that of *Spermatodus*. The dorsal margin of the angular is expanded in the central region, with some variation. One specimen has an expanded portion slightly anterior to that of the opposite angular. The articular surface near the posterior end has not been observed; the posterior end of the angular slopes off abruptly. The anterior sutures are seen in only two specimens, K. U. nos. 788, 11425. The dentary meets the angular in a long oblique suture; the dentary gradually tapers posterodorsally and ends on the dorsal surface of the angular. The splenial fits into a posteriorly directed, deep V-shaped notch on the ventral surface. The lateroventral surface of the angular contains sensory pores of the mandibular line. The ventral surface extends medially into a narrow shelf, approximately 1.0 mm. wide, which extends the full length of the bone; the external surface of this shelf is smooth and slightly concave dorsally. Ornamentation of the angular consists of tubercles and longitudinal or oblique striae, occurring mostly on the expanded portion. The medial surface is not seen. Several broken

specimens show a central canal filled with a rod of calcite; in one of these the sensory pores are also calcite-filled and appear to be connected to the rod. Thus the pores originally opened into a central canal.

The dentary is an unornamented bone with the anterior half curving medially; the greatest height is anterior. This bone in specimen K. U. no. 11425 bears irregularly spaced, simple, recurved, conical teeth; nine were counted, but there is space for many others. One other specimen, no. 11429, seems to have tiny tubercles on the surface. The dentary meets the splenial dorsally in a straight suture.

The splenial also curves medially, and as stated, meets the dentary in a straight suture. Ornamentation on this bone was not observed. The posterior margin is V-shaped and fits the notch in the angular. The ventral surface bears three or more sensory pores of the mandibular line.

The gular plates are oval. The medial margin is straight to slightly curved, the lateral margin curved crescentically, the posterior end is blunt, and the anterior end somewhat rounded. Ornamentation varies greatly; some bones show only a few tubercles, whereas others exhibit an almost concentric pattern of closely spaced striae. Typically there are some tubercles in the anterior quarter or third of the total length; these pass into longitudinally oriented striae in the posterior section. A few have only randomly oriented, widely-spaced striae. The internal surface is smooth.

The coronoid (K. U. no. 11428) is a triangular bone, with the apex pointing dorsally. The lateral surface is smooth; no teeth were observed. Moy-Thomas (1937:292, 293) mentions several tooth-bearing coronoids in *Rhabdoderma*, but as yet these have not been seen in *Synaptotylus*.

Axial skeleton

Only three specimens (K. U. nos. 786F, 787F, 11450) show parts of the vertebral column, but isolated neural and haemal arches are numerous. All are of the coelacanth type, having Y-shaped neural and haemal arches, without centra. A total count of 38 was obtained, but this was incomplete; the actual number was probably near 50. Counts of 10 and 16 haemal arches were obtained in two of the specimens. Total height of neural arches ranges from 7.5 to 12.0 mm., and of haemal arches, from 9.0 to 12.0 mm. The shorter arches are anterior and the height increases gradually to a maximum in the caudal region. Height of the spines varies from

4.0 to 9.0 mm., or from twice the height of the arch in the anterior to three times the height in the caudal region. Total width of the base, measured in isolated specimens because lateral views in other specimens prevented measuring width, ranges from 0.7 to 4.2 mm. The short, broad arches having short spines occur at the anterior end of the spinal column; the narrower arches having tall spines occur toward the caudal end. Broken neural and haemal arches show a thin covering of bone with a central, calcite-filled cavity, which in life may have been filled with cartilage (Stensiö, 1932:58, fig. 20).

No ossified ribs have been observed, either isolated or in place. For further description of the axial skeleton, see Hibbard (1933).

Girdles and paired fins

A nearly complete pectoral girdle on specimen K. U. no. 11433 (see fig. 6A) has only a cleithrum and clavicle. No evidence of an extracleithrum or supracleithrum has been observed, but the extracleithrum may be fused to the cleithrum. The two bones form a boot-shaped unit, with the anteroventral part turned medially to form a horizontal process which meets the opposite half of the girdle. In lateral view the surface is unornamented, and convex in the ventral half. The suture between the cleithrum and clavicle begins on the expanded posterior portion, the "boot-heel," at a point immediately below the greatest width on the posterior margin,

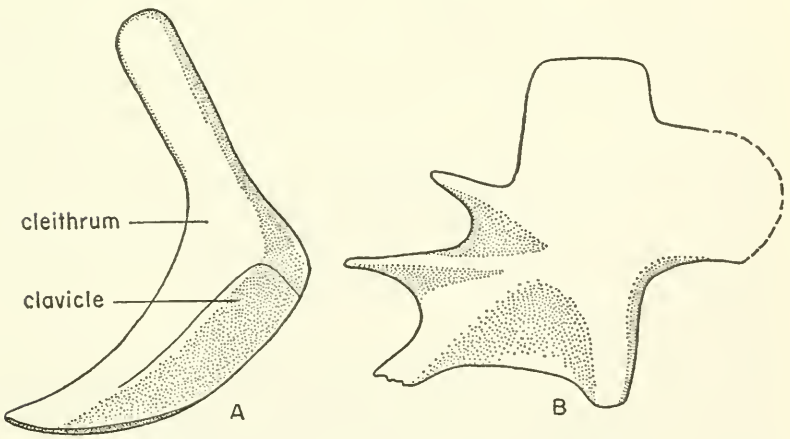

Fig. 6. *Synaptotylus newelli* (Hibbard). Paired fin girdles. A, pectoral girdle, lateral view, based on K. U. no. 11433, × 3.5. B, pelvic girdle basal plate, medial (?) view, based on K. U. no. 788, × 8. Anterior is toward the left.

passes anteriorly, then turns sharply and parallels the anterior margin. The shape of the cleithrum resembles that in *Rhabdoderma* and the internal surface is not ridged (see Moy-Thomas, 1937:fig. 9). The exact orientation in the fish is uncertain, but if the median extension is really horizontal, then the posterior expansion is directed caudally. The medial surface is concave, steepest near the anterior margin, and then slopes outward evenly. In medial view one specimen (K. U. no. 11426) shows a small, caudally directed projection of bone, evidently for articulation of the fin-skeleton, at the widest portion of the cleithrum. Sutures on several specimens were indistinct. Broken specimens show sutural faces, but many nearly complete specimens show little or no indication of sutures, without regard to size of the girdles. The internal structure of the fin was not observed.

Numerous isolated basal plates of the pelvic girdle have revealed details of structure but no information on the orientation. Presumably the basal plates of *Synaptotylus* had essentially the same orientation as those of other coelacanths (Moy-Thomas, 1937:395). The most complete basal plate is K. U. no. 788 (see fig. 6B). The three apophyses diverge anteriorly; the horizontal one is best developed and the dorsal one is least well developed. A median process (Schaeffer, 1952:49), denticulate on several specimens, articulates with the corresponding process of the opposite plate. The expanded part that articulates with the skeleton of the fin extends caudally. The posterior expanded part is nearly square in outline, resembling the dorsal, rectangular projection. One side bears ridges leading to the extremities of the apophyses, and faint crenulations on the median process. This may be the medial view. The other view displays a smooth surface, usually without indication of the ridges seen in the reverse view. These specimens differ somewhat from the basal plates of *Rhabdoderma* and appear to be intermediate between *Rhabdoderma* and *Coelacanthus* (Moy-Thomas, 1937:fig. 10A, B). The apophyses are not free as in *Rhabdoderma* but webbed with bone almost to their extremities, as in *Coelacanthus*.

The pelvic fin is seen in only two specimens (K. U. nos. 786F, 788). That on no. 788 is lobate and has 25 lepidotrichia, jointed for approximately the distal half, and 2.5 to 13.0 mm. in length. Total length of the fin is 25.0 mm. There is no trace of the internal skeletal structure or of the articulation to the basal plate in either specimen. For a description of the fin on no. 786F, see Hibbard (1933:281).

Unpaired fins

A few isolated bones on K. U. no. 788 (fig. 7) are interpreted as basal plates of the unpaired fins. For additional description of the unpaired fins on the type, K. U. no. 786F, see Hibbard (1933).

Two of these bones are flat, smooth and oblong, bearing a diagonal ridge that extends in the form of a projection. Orientation is completely unknown. These may be basal plates of the anterior dorsal fin. The fin on no. 786F that Hibbard (1933:281) interpreted as the posterior dorsal fin is now thought to be the anterior dorsal fin.

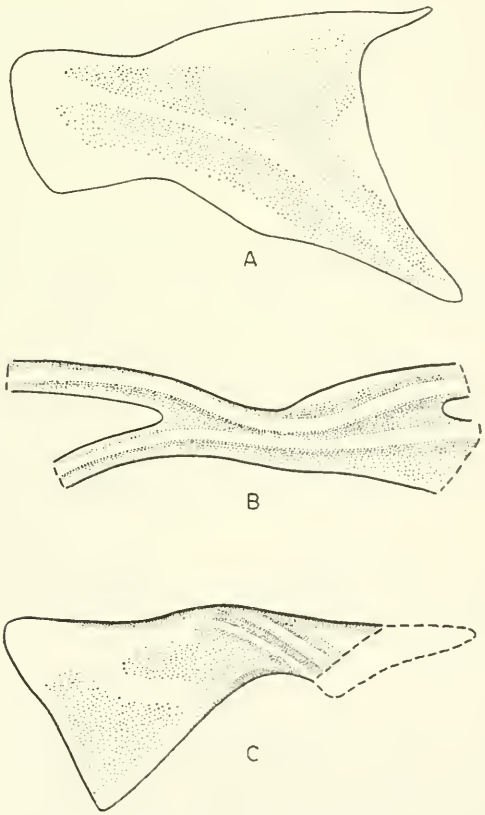

Fig. 7. *Synaptotylus newelli* (Hibbard). Basal plates of unpaired fins. A, anterior dorsal fin, based on K. U. no. 788, × 10. B, posterior dorsal fin, based on K. U. no. 788, × 12. C, anal fin, based on K. U. no. 11450, × 5. Anterior is toward the left.

One distinctive bone may represent the basal plate of the posterior dorsal fin. This incomplete specimen shows two projecting curved processes, bearing low but distinct ridges, which diverge, probably anteriorly. The central portion is narrow. The two ridges continue onto the posterior portion. This has been broken off, but shows that the ridges diverge again. The surface is smooth, except for the ridges. As before, orientation is uncertain. On no. 786F this fin was interpreted by Hibbard (1933:281) as the anal fin.

Only part of one basal plate of the anal fin was preserved on K. U. no. 11450. That plate is oblong and has an expanded anterior end. The narrow, constricted part bears two oblique ridges and a few tubercles. The posterior part has nearly straight margins (represented by impressions) and the posterior margin is oblique, sloping anteroventrally. The flared anterior part has a smooth surface. This basal plate is more nearly like those of *Coelacanthus*, according to the descriptions given by Moy-Thomas (1937:399). The basal plate is associated with seven apparently unjointed, incomplete lepidotrichia. The anal fin on no. 786F is interpreted as the anterior dorsal fin (Hibbard, 1933:281).

The caudal fins are preserved on K. U. nos. 786F, 787F, and have a total of 24 lepidotrichia, 12 above and 12 below. These are jointed for the distal half or two-thirds, and are up to 16.0 mm. in length. In specimen no. 787F the supplementary caudal fin has at least seven lepidotrichia, the longest of which is 11.0 mm. but incomplete. Anterior lepidotrichia appear unjointed but the posterior ones are jointed for the distal two-thirds (?) (these are broken off). The supplementary caudal fin is approximately 1.5 mm. long and 8.0 mm. or more wide. The supplementary caudal fin on K. U. no. 786F described by Hibbard (1933:281) could not be observed; this part of the caudal fin is missing.

Squamation

In the suite of specimens isolated scales are numerous, but patches of scales are rare. Only two specimens (K. U. nos. 786F, 787F) are complete enough for scale counts, but preservation permits only partial counts. In general the scales resemble those of *Rhabdoderma elegans* (Newberry).

The scales are oval. The exposed posterior part of each bears posteriorly converging ridges; the anterior part is widest and shows a fine fibrillar structure. There are at least six scale-rows on either

side of the lateral line. Lateral line scales show no pores, and except for slight irregularities in the orientation and length of the posterior ridges, closely resemble the others. Central ridges on the lateral line scales are shorter and tend to diverge from the center of the impression of the canal. The lateral line canal shows only as the impression of a continuous canal 0.7 mm. in diameter. Preservation is poorest in scales along the line of the neural and haemal arches; therefore lateral line scales are rarely preserved. Isolated scales are of two types: those on which the posterior ridges converge sharply and form the gothic arch configuration mentioned by Hibbard (1933:282), and those which do not. Both types of scales can be present on one fish, as shown by specimen no. 788. This is not apparent on nos. 786F and 787F; all of the scales on these specimens appear to be much alike. Both Moy-Thomas (1937:385) and Schaeffer (1952:51, 52) have remarked on the variation of the scales on different parts of the same fish. Because the number of ridges and amount of convergence of the ridges is not related to size of the scale, it is concluded that these characters are not of taxonomic significance.

The strong resemblance of the scales of the Garnett specimens to those of *Rhabdoderma elegans* (Newberry) caused Moy-Thomas (1937:399) to add Hibbard's two species to the synonymy of *R. elegans*. But at that time only the scales could be adequately described. If the shape of the scale and the number and pattern of ridges can vary with age, size and shape of the scale, it follows that assignment of isolated scales to a species should not be attempted. Assignment to genus should be made only with caution.

Discussion.—The relationship of *Synaptotylus* to other coelacanths is obscure at present. The knoblike antotic processes on the basisphenoid are unlike those of any other known coelacanth. The palatoquadrate complex is shaped like that of *Rhabdoderma elegans* but consists of fewer bones, probably because of fusion. The scales resemble those of *Rhabdoderma*. With regard to general shape of fin girdles, the pectoral girdle resembles that of *Eusthenopteron* more than that of *Rhabdoderma*, but the cleithrum is more nearly like the cleithrum of *Rhabdoderma*. The pelvic girdle appears to be midway between those of *Rhabdoderma* and *Coelacanthus* in general appearance. Regarding the basal plates of the remaining fins, those of *Synaptotylus* appear to resemble basal plates of both *Rhabdoderma* and *Coelacanthus*. Considering the structure of the sphenethmoid region of the braincase, *Synaptotylus* is probably

more closely related to *Rhabdoderma* than to other known coelacanth genera.

COMMENTS ON CLASSIFICATIONS

Classification of Carboniferous coelacanths has been difficult, partly because the remains are commonly fragmentary, and significant changes in anatomy did not become apparent in early studies. In general, coelacanths have been remarkably stable in most characters, and it has been difficult to divide the group into families. As Schaeffer (1952:56) pointed out, definition of coelacanth genera and species has previously been made on nonmeristic characters, and the range of variation within a species has received little attention. For example, Reis (1888:71) established the genus *Rhabdoderma,* using the strong striation of the scales, gular plates and posterior mandible as the main characters of this Carboniferous genus. Moy-Thomas (1937:399-411) referred all Carboniferous species to *Rhabdoderma,* redescribed the genus and compared it to *Coelacanthus,* the Permian genus. He cited as specific characters the ornamentation of the angulars, opercular and gular plates (Moy-Thomas, 1935:39; 1937:385). Individual variation in some species has rendered ornamentation a poor criterion. This variation is apparent in *Synaptotylus newelli* (Hibbard), some specimens having little or no ornamentation; others having much more. The number of ridges and pattern of ridges on the scales also varies. Schaeffer (1952:56) has found this to be true of *Diplurus* also. Moy-Thomas (1935:40; 1937:385) realized that the type of scale is a poor criterion for specific differentiation. In the search for features useful in distinguishing genera of coelacanths, Schaeffer and Gregory (1961:3, 7) found the structure of the basisphenoid to be distinctive in known genera, and thought it had taxonomic significance at this level. Higher categories should have as their basis characters that display evolutionary sequences. A recent classification (Berg, 1940), followed in this paper, reflects two evolutionary trends in endocranial structure of coelacanths: reduction of endocranial ossification and loss of the basipterygoid processes. Because there has been little change in other structures in coelacanths, Berg's classification is the most useful. Berg (1940:390) includes *Rhabdoderma* in the suborder Diplocercidoidei because of the presence of the basipterygoid processes, and in the single family, Diplocercidae, but remarks that because of the reduced amount of endocranial ossification the Car-

boniferous Diplocercidae "probably constitute a distinct family." In considering this concept of classification, the subfamilies Diplocercinae and Rhabdodermatinae of the family Diplocercidae are proposed above. The subfamily Rhabdodermatinae includes at present *Rhabdoderma* and *Synaptotylus*. The principal characters of the subfamily Rhabdodermatinae, named for the first known genus, are the retention of the basipterygoid processes and the reduction of endocranial ossification. Application of this classification based upon endocranial structure would probably change existing groupings of species of Carboniferous coelacanths; the entire complex of Carboniferous genera should be redescribed and redefined. It will be necessary to consider endocranial structure in any future classification.

The greater part of the evolution previously mentioned appears to have been accomplished during the Carboniferous; thereafter coelacanth structure became stabilized. The trend progressed from Devonian coelacanths which had two large unpaired bones in the endocranium, and both antotic and basipterygoid processes on the basisphenoid, to Carboniferous fishes in which ossification was reduced to a number of paired and unpaired bones embedded in cartilage, and retaining both processes, and then post-Carboniferous kinds with reduced ossification and no basipterygoid processes. The Pennsylvanian was evidently the time of greatest change for the coelacanths, and they have not changed significantly since, in spite of the fact that since the Jurassic they have shifted their environment from shallow, fresh water to moderate depth in the sea (Schaeffer, 1953:fig. 1). The changes in endocranial structure appear to be significant, and are perhaps related to higher efficiency of the mouth parts in catching and swallowing prey (see p. 482).

ENVIRONMENT

The coelacanth fishes from the Rock Lake shale are part of the varied fauna collected from Garnett. Peabody (1952:38) listed many elements of the fauna and flora, and concluded that the deposits are of lagoonal origin. In addition to numerous invertebrates (including microfossils) and arthropods, a number of vertebrates other than coelacanths have been found. These include at least one kind of shark, *Hesperoherpeton garnettense* Peabody, one or more kinds of undescribed labyrinthodonts and the reptiles *Petrolacosaurus kansensis* Lane, *Edaphosaurus ecordi* Peabody, and *Clepsydrops* (undescribed species). This is indeed a rich vertebrate

fauna, and the earliest known reptilian fauna. Much of the rock contains plant remains. The flora that has been identified is adapted to growing in a well-drained soil; although it contains some elements considered characteristic of the Permian, it is of Pennsylvanian age (Moore *et al.*, 1936). Peabody (1952:38-39) discusses the features of these lagoonal sediments. Much of the fauna and flora suggests continental origin, but the many marine invertebrates at some horizons indicate that at least some of the sediments were of marine origin.

Little can be said about the actual environment of the living fishes of the genus *Synaptotylus*. Remains of these fishes occur in layers containing marine invertebrates, as well as in those containing plant remains and vertebrate skeletal parts, and in those nearly completely composed of dark carbonaceous material. Most of the remains are fragmentary and consist of isolated bones, isolated scales, and dissociated skulls; only one specimen and half of another are nearly complete. Many published statements on *Rhabdoderma*, a related genus, indicate both marine and fresh-water environments. Wehrli (1931:115) regarded *Rhabdoderma elegans* (Newberry) as a euryhaline species, and cited its occurrence with both marine and fresh-water fossils. Aldinger (1931:199) also found this to be the case with other species, and Fiege (1951:17) quotes others as giving the same information. Keller (1934:913) thought that few Carboniferous fishes were exclusively marine, and stated that the majority of them became adapted to fresh water during the late Carboniferous. Later, Schaeffer (1953:175) stated that all Carboniferous and Permian coelacanths were fresh-water fishes, and that many were from swamp deposits. If Keller is correct, then members of the genus *Synaptotylus* may have inhabited the lagoon, the adjacent sea, or the streams draining into the lagoon. Perhaps these fishes swam upstream, as modern salmon and tarpon do, although there is no direct evidence for this. Possibly they lived in the lagoon at times of scant rainfall and little runoff, when the salinity of lagoon water approached normal marine values or the fishes may have lived in the streams, and after death were washed into the lagoon. As numerous remains of land plants and animals were washed in, perhaps this best accounts for the presence of the fish in nearly all layers of the deposits, not only the marine strata.

SUMMARY

A new genus of Pennsylvanian coelacanths, *Synaptotylus*, is described and a previously named species, *Coelacanthus newelli* Hibbard, 1933 (*C. arcuatus* Hibbard, 1933, is a junior synonym), is referred to this genus. All specimens of *Synaptotylus newelli* (Hibbard) were collected from the Rock Lake shale member of the Stanton formation, Lansing group, Missouri series, six miles northwest of Garnett, Anderson County, Kansas. *Synaptotylus* is distinguished from all other coelacanths by a basisphenoid having large, knoblike antotic processes each connected by a low ridge to a small basipterygoid process. *Synaptotylus* is most closely related to *Rhabdoderma*, but is intermediate between *Rhabdoderma* and *Coelacanthus* in shape of the fin girdles and basal plates. Two new subfamilies, Diplocercinae and Rhabdodermatinae, of the family Diplocercidae, are proposed. *Synaptotylus* and *Rhabdoderma* are included in the subfamily Rhabdodermatinae, because both exhibit reduced ossification in the endocranium and retain basipterygoid processes.

Loss of the basipterygoid processes in post-Carboniferous coelacanths may reflect the development of a more efficient feeding mechanism, by allowing the palatoquadrate complex and mandible to swing farther laterally and expand the oral cavity.

Synaptotylus newelli (Hibbard) may have occupied either the sea or fresh water; these fishes occur in lagoonal deposits with reptiles and amphibians, arthropods, marine invertebrates and remains of land plants.

Because scale patterns on *Synaptotylus* and *Rhabdoderma* are so nearly similar and vary with size of the scale and its location on the fish, it is recommended that isolated scales not be assigned to a species, and to a genus only with great caution.

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Observations on the Mississippi Kite in Southwestern Kansas

BY

HENRY S. FITCH

The Mississippi kite (*Ictinia misisippiensis*) is one of the common raptors of Kansas, occurring regularly and abundantly in summer in that part of the state south of the Arkansas River. In 1961, in an attempt to find out more about the ecology of the species in Kansas, I made several trips to parts of the state where kites could be found in numbers, notably to Meade County State Park in the southwestern part of the state, 7½ miles south and five miles west of Meade. Little has been written regarding the species in this extreme northwestern part of its breeding range, where it thrives under ecological conditions much different from those that prevail elsewhere in its range. Also, the social behavior and food habits have been given relatively little attention.

In my field study I was helped by my son, John H. Fitch, who climbed to many kite nests and spent many hours observing in the field. My daughter, Alice V. Fitch, likewise aided me by keeping nests under surveillance. Dr. Claude W. Hibbard of the University of Michigan and Mr. Harry Smith, superintendent of Meade State Park, also kindly provided much useful information concerning the history of the colony of Mississippi kites at the Park. Mr. William N. Berg analyzed pellets, and Dr. George W. Byers kindly checked many of the identifications, and provided generic and specific determinations for some of the insects.

In general, the range, habits and ecology of the Mississippi kite are already well known through the publications of Audubon (1840), Chapman (1891), Bendire (1892), Ganier (1902), Wayne (1910), Nice (1931), Bent (1936), Sutton (1939) and Eisenmann (1963). The breeding range is the southeastern United States, chiefly within the Austroriparian Life-zone, but extending northwest through much of Oklahoma and into southern Kansas. The species is highly migratory. Wintering Mississippi kites are known from Argentina and Paraguay (Eisenmann, *op cit.*:74), and most of the population probably winters in southern South America, but records outside the breeding range are few.

The Mississippi kite is perhaps one of the most social raptors. It is highly gregarious, not only in its migrations but in breeding

colonies. All breeding pairs seen were closely associated with other individuals, with no territorial hostility; signs of intraspecific intolerance are rare, even where the kites are abundant. In the nesting season many of both sexes perch together in the same tree, and groups tend to keep together as they forage.

Secondary sexual differences are slight. Seven males in the University of Kansas Museum of Natural History collection average 351 (342 to 360) millimeters in length, and six females average 361 (348 to 370) millimeters. Sutton (*op. cit.*:44) collected 16 breeding kites near Arnett, Oklahoma in 1936 and 1937 and recorded that eleven males averaged 245 (216 to 269) grams and five females averaged 311 (278 to 339) grams. As indicated by Sutton, the head is paler in the adult male than in the female, and at close range this difference will serve for identification of the sexes. The difference in size is scarcely noticeable in the field.

Habitat

In Kansas this kite seems to prefer open and even barren terrain, in contrast with its habitat in forests of the southeastern states. Typical habitat of Kansas is that of the High Plains, dominated by a short-grass climax of blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*), with sagebrush (*Artemisia* sp.), prickly pear (*Opuntia* sp.) and other somewhat xerophytic vegetation. In the Gypsum Hills of south-central Kansas near the Oklahoma border, the Mississippi kite finds habitat conditions exceptionally favorable. This is an area of broken topography, dissected by small steep-sided ravines, often with brush and scrubby trees on the slopes.

At Meade County State Park groves of cottonwoods (*Populus deltoides*) provided abundant places for perching and nesting. At this locality an artesian well provided an abundant year round water supply, which was impounded into an artificial lake half a mile long and a little less than a quarter mile wide. Water was also impounded in a series of small ponds maintained for the benefit of fish and waterfowl. Along with other improvements extensive plantings of cottonwoods and other trees were made with relief labor in the nineteen thirties. Trees were scarce on the area originally, but by 1961 there were almost continuous groves in an area nearly two miles long and three quarters of a mile wide encompassing the lake and ponds and adjacent areas. In conversation at the Park in August 1961, Dr. C. W. Hibbard told me of his observations on the colony of kites since 1936 when his paleonto-

logical field work in that area was begun. He indicated an area of less than two acres west of the artesian well to which the colony had been limited in its nesting in 1936, because at that time few trees were available as nest sites. In subsequent years, as the trees in the artificially established groves increased in size and height, and other trees became established naturally where the impoundments had created favorably moist conditions, the nesting colony expanded in all directions, and the number of kites increased tremendously. When my observations were made in 1961, the nesting area was co-extensive with the cottonwood groves, and there were literally thousands of trees within the area that provided adequate sites for nests.

Numbers

The maximum number of kites seen flying at one time at the Park was 44, on August 22, 1961. Probably almost all there were adults, because fledglings, even though able to fly strongly by this date, were still spending most of their time perched. The colony of kites was usually scattered over at least two square miles, and at most times some were perched, others were flying low and solitarily, hence it is improbable that the total population or a high percentage of it could be seen together at any one time or place. More than 40 nests were located in 1961, and probably at least as many more were overlooked. There must have been a breeding population of at least 100 kites, and probably as many as 150 in the Park in 1961. H. B. Tordoff recorded on the label of K. U. Mus. Nat. Hist. no. 30514, taken on September 1, 1951, in Barber County, Kansas, that it was one of at least 200 at a communal roost.

Feeding

The Park and its vicinity stood out as a veritable oasis in an almost treeless region of open rolling topography, with a short-grass type of vegetation dominating. The kites displayed versatility in their choice of places to forage. Often they soared over the cottonwood groves, the lake, or the ponds, but at other times they flew far out over the plains, and seemed to prefer such open situations. A small herd of buffalo was maintained at the Park, and their closely grazed pastures of several hundred acres were favorite foraging grounds for the kites. Often the kites and buffalo were seen in close association, and at times the kites must have benefited from the movements of the buffalo, serving to flush certain insects such as grasshoppers. The latter were probably the chief food source of the kites in the heavily grazed pastures. Bent (1936:67) stated:

"A flock of from 3 to 20 will sail about a person, a horseman or a team, traveling through grassy flats or bushy places, and seize the cicadas as they are scared up." Dr. Hibbard told me that on one occasion when he had caught a number of cicadas, he fed them to a pair of kites by tossing them into the air one by one, and each was seized by a kite which was flying nearby waiting expectantly.

Mississippi kites are noted for their buoyant and seemingly almost effortless flight, and their prey is caught while they are on the wing. In extended flights the kites soar, drift and circle with frequent easy flapping, at variable heights. Sometimes they are several hundred feet above the ground. Doubtless the height is influenced by the types of insects that are flying, and where they can be found most readily. Even at close range the catching of prey by a kite is likely to be overlooked by an observer. After being snatched from the air, the prey is usually eaten while the kite is still in flight, and the movements of the head in pecking at the objects held in the talons are much more noticeable than the slight veering from the course of flight that signals the actual capture. Kites were often watched while they were hunting in the open areas around the Park. On June 1, 1961, my son and I observed 16 perched together in a small tree. From time to time each kite would leave the tree in a short flight low over the surface of a nearby pool, where it would snatch up prey, probably a dragonfly in many instances, and would return to a perch to feed. Most of the time one or several kites were in flight while the majority were perched. Similar observations were made on smaller groups perched on fence posts along the edges of large pastures. Gregarious tendencies were evident from the fact that two or more of the kites perched fairly near together on separate but sometimes adjacent fence posts. Each kite in turn would glide from its post, skim low over the ground surface for a few seconds, seize its prey with a sudden slight swerving, and return to the fence (usually to a different post from the one it had left) to feed upon the insect captured. Grasshoppers of many species were abundant in the area. It seemed that grasshoppers were flushed from the ground by the bird flying near them and were picked off before they were well underway. In any case the prey was taken from the air rather than from the ground in all observed instances. Ganier (1902:86) mentioned seeing one of these kites alight on the ground in a cotton field, where it stayed for more than a minute, but perching on the ground is unusual.

Most often kites that were catching their prey by skimming close

to the ground did not return to a perch but ate while they were flying. Associations of groups on posts at edges of fields, in trees or in flight were ephemeral as each bird seemed driven by a restless urge to be in motion. The kites generally gave the impression of catching their prey effortlessly and casually in the course of their flights. However, on July 20, 1961, one flying over a pond was seen to swoop three times in rapid succession at a dragonfly without catching it. The kite then flew higher, circled, and swooped three times more at the dragonfly, catching it on the last attempt. Most of the insects preyed upon are slower and less elusive than dragonflies, which are largely immune to the attacks of flying predators because of their great prowess in flight.

Only on rare occasions could the kind of prey captured be observed in the field. Food habits were studied by collecting pellets of the kites at the Park, and analyzing them. The pellets were usually disgorged early in the morning while the kites were still on their night roosts in large cottonwoods. Often several kites roosted in the same tree. The pellets were of characteristic appearance, elliptical, approximately 15 millimeters in diameter, 30 millimeters long, pinkish or purplish, composed of insects' exoskeletons compacted, and comminuted to about the consistency they would have after passing through a meat grinder.

A total of 205 pellets was collected—37 on August 20, 1960; 56 on July 18, 1961; 60 on August 4 and 5, 1961, and 52 on August 21 to 23, 1961. A total of 453 separate items was tentatively identified. Obviously the material was far from ideal for the identification of prey, which had to be reconstructed from minute fragments. The kites are dainty feeders and discard the larger and less digestible parts such as wings, legs, and heads. Often it was uncertain how many individuals or how many kinds of insects were represented in a pellet. Probably most pellets contained many individuals of the same species, but these were not separable. Hence, only 2.2 items per pellet were found, whereas Sutton found an average of 22.2 items in each of the 16 stomachs that he examined.

Best information concerning kinds of prey utilized was obtained soon after the fledglings had left the nest; on various occasions these still clumsy young dropped nearly intact insects that were delivered to them by the adults. These insects, recovered from beneath the perches, were the basis for all specific and generic determinations; other material was determinable only to order or to family.

One of the most significant outcomes of the examination of pellets

was the finding that vertebrates were scarcely, if at all, represented in the food. Three pellets contained shreds that seemed to be mammal hairs, but in the absence of other remains, the diagnosis is somewhat doubtful. Many species of small mammals, birds, reptiles and amphibians were common in the Park or its vicinity, but insects made up nearly all the recorded prey. Audubon (1840: 73) mentioned lizards and small snakes in the food and gave a dramatic but perhaps imaginative account of a kite swooping and snatching a lizard (anole) from the topmost branch of a tree. Goss (1891:251) stated: "I have seen them swoop down, and, with their claws, snatch lizards from the ground, rocks and old logs, sometimes stopping to eat them, but, as a rule, feeding on the wing." Bendire (1892:179) stated that the food was mostly insects "probably varied with a diet of small rodents, lizards and snakes." Wayne (1910:71) stated that the food consisted almost entirely of insects and lizards. Bent (1936:67-68), after stating that small snakes, lizards and frogs were sometimes taken, cited a statement in the notes of G. W. Stevens that the latter had found the remains of toads, mice and young rabbits in nests with young. However, Sutton (*op cit.*:51) in a detailed analysis of the stomach contents of 16 kites in Oklahoma, found only insects and remains of one small fish among a total of 358 prey items. Predation on vertebrates must be rare, and perhaps requires further verification in view of the rather vague character of the records so far published.

The following list includes both the prey found beneath perches of fledglings and that identified from pellets, the latter mostly from adult kites.

- coleopteran
  - unspecified 187
  - carabid 39
  - cicindelid
    - unspecified 18
    - *Cicindela* sp. 2
  - hydrophilid
    - unspecified 18
    - *Hydrous* sp. 1
  - scarabaeid
    - unspecified 1
    - *Canthon* sp. 3
  - silphid
    - *Necrophorus* sp. 1
- orthopteran
  - unspecified 120
  - locustid
    - unspecified 34
    - *Arphia crassa* 1
    - *Melanoplus* cf. *differentialis*, 2
    - *Schistocerca* cf. *lineata* 1
    - *Xanthippus corallipes* 2
  - tettigoniid
    - unspecified 3
    - *Daihinia* sp. 1
- homopteran
  - cicadid
    - unspecified 15
    - *Tibicen* cf. *pruinosa* 1
- lepidopteran (unspecified moth), 3

At Meade State Park I gained the impression that much of the foraging is carried on near the nest. The short time lapse between successive feedings was one indication, and from time to time while keeping nests under observation, I saw kites that were individually recognizable as the owners coursing back and forth in the vicinity. However, only a few individuals were recognizable. For several minutes before and after delivering food, such an adult was often seen soaring within 200 to 300 yards of the nest, or sometimes much closer. A somewhat different impression was received on August 23, 1961, at Natural Bridge, south of Sun City, Barber County, Kansas, where I observed two pairs of kites feeding fledglings. One fledgling was seen to be fed ten times in a 1½ hour period. The transfer of food from the adult usually required less than a minute. Then the adult would leave the tree, in a ravine, and drift away. Circling and soaring, it seemed to be wandering aimlessly, but within two or three minutes it was usually out of sight over the horizon. In what appeared to be slow, lazy, flight it usually drifted off to the west, to more upland areas of short grass and sage brush. Once, watching from a high knoll I succeeded in keeping it in view for almost five minutes, and during most of this time it appeared to be between one and two miles away, but it finally moved off even farther. Dr. Hibbard mentioned seeing kites in the vicinity of the Jinglebob Ranch eight to ten miles from the Park, and he believed that these individuals had come from the Park since there was no suitable habitat in the intervening areas. Actually, the distance could have been covered in a few minutes' flying time, but it is unlikely that these individuals were feeding young at the Park, else they would not have wandered so far. On several occasions groups of from three to 20 individuals were seen in open terrain as much as four or five miles from the Park.

Breeding Cycle

Probably kites arriving from their northward migration are already paired. In those observed at the Park in the first week of June, there was no indication of courtship, or of sexual rivalry. On June 1, 1961, incubation had begun. The birds had arrived some three weeks earlier, according to Smith. Although arriving from the south long after most raptors have begun their nesting, the kites are not further delayed by establishment of territories and choosing of mates, and nesting is underway soon after their arrival.

According to Sutton (1939:45) the nest-building is an exceedingly leisurely process. In the first two weeks after their arrival he observed that the kites only occasionally bring a twig to the nest, usually repairing last year's structure rather than starting a new one. Sutton recorded egg-laying on May 17 and 18 and hatching on June 18 in northwestern Oklahoma, and the timing of these events must be similar in Meade County, Kansas.

Shortly before sunset on June 1 a pair was observed at close range from a parked automobile as the kites perched on roadside fence posts about 50 feet apart at the Park boundary. At this time the birds lacked their usual restlessness and were perching quietly, neither preening nor attempting to find prey. With no preliminaries the male flew to the female and lit on her back to copulate. The female was receptive but did not crouch in a horizontal position. The mounting lasted for approximately a minute. During the first 30 seconds the male was fully occupied with balancing and positioning himself, and copulation occurred only during the latter half of the mounting. During this interval cloacal contact was effected three times, but was only momentary each time. The birds were silent. After the male left, the female continued to perch until flushed by my movements.

Judging from the nests that were examined, the kites of the Meade Park area are well synchronized in their nesting, as all arrive at approximately the same time. Bent (1936:66) stated that if a kite's nest is robbed, the birds will lay a second set, either in the old nest or a new one, about two weeks later. All young seen at Meade State Park seemed to represent an age range of considerably less than two weeks, and, presumably, no renestings were involved.

Nests were variable in size. Some were remarkably small in relation to size of the kites, and would scarcely have been credited to this species, had not the kites been seen sitting on them. Nests were from 10 to 18 (average 14) inches long and from 10 to 14 (average 11.7) inches wide, in forks or crotches of branches. The branches supporting the nests were from 1½ to 10 inches in diameter. The nests were constructed of twigs of approximately pencil size. Of 37 nests at the Park, 29 were in cottonwoods, six were in willows, and two were in elms. The figures probably reflect the relative numbers of each of these species of tree rather than any clear-cut preference of the kites. By the time nesting has begun the trees have leafed out, and the nests are well concealed.

At the time of my visit to the Park, July 18 to 22, nestlings were well grown, and were beginning to feather out. On August 4 and 5 the young were well feathered, but flight feathers were not fully grown and the young remained in the nest or perched on nearby branches. On August 21 to 24 the young were fully fledged, and were able to fly strongly but they still spent most of their time perching and those of a brood tended to stay near together, usually in the nest tree.

In a total of 26½ hours of observation, 148 feedings were observed —on the average one per 10.7 minutes. The interval changed from an average of 12.8 minutes for 62 feedings on July 19 to 21, to 8.5 minutes for 59 feedings on August 4, and to 10.8 minutes for 27 feedings on August 21. The longer interval on July 19 to 21 may have resulted from the greater furtiveness of the adult kites at this stage in their nesting cycle. Nests usually were watched through field glasses at distances of 50 to 100 feet. Ordinarily kites are not disturbed by the presence of a person at these distances, but when delivering food to the nest they seemed somewhat distracted and sometimes stopped only momentarily then left, still carrying the food. Usually they swooped at the observer when leaving; rarely they swooped at him as they approached the nest. All observations were between 10 a. m. and 5 p. m., and there was no obvious trend according to time. Earlier and later in the day the rate of delivery is probably less. The kites are notably late risers, and their activity increases gradually after sunrise; in late afternoon activity tapers off again. In 89 feedings, the average visit to the nest lasted 51 seconds but this average included a few relatively long stops, up to four minutes in length, and 60 per cent of the visits were for intervals of 30 seconds or less.

Insects often protruded from the bills of the adult kites delivering food, but most of the food was carried in the throat. Sometimes the gorge was much distended, although nothing protruded from the mouth. The adult upon alighting sometimes would pass food to the nestling, and sometimes would disgorge a mass of food in the nest in front of the nestling. When the young were small, the adult after having disgorged a food mass, remained to pick up the food, bit by bit, and place it in the mouth of the nestling. However, after the young were partly feathered out the adult merely left the food for them. The nestling sometimes would peck at the disgorged material for several minutes after the adult left before all of the food was eaten.

The small nestlings are generally silent, but when handled or otherwise disturbed, they give soft lisping peeps. By early August, when the young have ventured from the nest bowl to nearby branches, they become vocal and their calls can be heard more often than those of the adults. The call of the adult has been well rendered by Sutton (1939:43) with the syllables "phee phew"—a whistle in which the first syllable is short (lasting only about one-fourth of a second) with a rising inflection, clipped off short, while the second syllable has a downward inflection, and is drawn out to two or three times the length of the first syllable. The call of the fledgling is soft, with a lisping quality; that of the adult is much like it but is sharper and more piercing. Fledglings call frequently while waiting to be fed, but as an adult approaches with food, the calls are given in rapid succession and slurred to a high thin squablike sqeaking or squealing.

When fledglings are able to fly and have left the nest, the adults generally pass food to them directly, rather than dropping the regurgitated mass, which might fall to the ground and be lost. On August 22 a fledgling was seen following an adult in flight, and was also seen to eat while it was flying. At this stage, when an adult fed one young of a brood, the other would sometimes fly to the spot in an attempt to share the meal. However, the transfer of food was usually rapid and the adult would leave within a few seconds. Young often were seen to fly out from the nest tree and maneuver in the vicinity, flying in a roughly circular course perhaps 100 feet in diameter and then returning to the nest tree, thereby familiarizing themselves with their surroundings.

According to the consensus of published accounts, there are usually two eggs per clutch, occasionally one or three. However, Ganier (1902:89), who studied the species in Mississippi, wrote: "Of all the nests I have examined [number unspecified] only one was found to contain more than a single egg." Nice (1931:69) recorded 19 sets of two each and seven of one each in Oklahoma. In the course of my observations, 12 clutches of two were recorded. A group of four fledglings were observed concentrating their activities at a nest more than 200 feet from any other known nests; possibly all belonged to the same brood, but this was not definitely determined.

Many of the nests that were in use in 1961 appeared to be relics from earlier years, as the material was darkened and disintegrating, but probably a new layer of sticks had been added on the top.

Bent (*op. cit.*:65) mentioned this kite's habit of frequently using the same nest in successive years. On one occasion as I drove over a little-used road in the Park and passed a cottonwood grove where kites were nesting, one of the birds swooped down and struck the top of the automobile. In a subsequent conversation, Harry Smith asked me if this had happened, and said that this particular kite had struck his truck frequently when he drove past its nest. This had occurred at the same place in three successive years, and Smith was convinced that the same kite had used the nest each year, although the bird was not recognizable except by its unusually aggressive behavior. On dozens of occasions in the course of my observations kites swooped at me when I was near their nests, but, except for this one individual, they always veered away at a distance of several feet or several yards.

At the time of my visit to the Park in early June, kites were relatively silent and secretive in their behavior. Approximately half of those that were incubating flushed when a person walked near the tree, but others continued to sit on their eggs until a person had climbed to within a few feet of the nest. Upon being flushed, such a kite, in 50 per cent of observed instances, swooped at least once at the intruder, but some of the kites would soar overhead, watching without making any active defense. At the time of my next visit, July 18 to 21, when the kites were feeding well grown nestlings, behavior at the nest was much different. As soon as a nest was located the parents began scolding and swooping. At the first nest observed, a group of eight kites had congregated within two minutes to scold and harass the intruders. Even kites whose nests were kept under observation frequently, never became fully reconciled to the intrusion but there was much difference between individuals in this respect. Some were reluctant to deliver food and, having secured prey, would fly about in the vicinity without coming to the nest.

Mortality Factors and Defense

Joint defense against a common enemy was noted on July 21, 1961, when 21 kites were seen swooping at a Swainson's hawk perched near the top of a large cottonwood, where it was partly protected by foliage and branches. When I flushed the hawk, it was pursued and harrassed by the kites, some of which followed it for nearly a quarter mile although there were no nests of the kites nearby. On August 4 a group of six kites was seen heckling

a fledgling Swainson's hawk, which crouched among thick foliage in the top of a tall cottonwood, as the kites swooped at it, sometimes brushing it with their wings when they swept past. Dr. Hibbard mentioned an instance in which a horned owl was flushed, and was chased and heckled by a red-tailed hawk and by a group of kites. The latter seemed to regard the owl as the greater enemy, but ordinarily any large raptor arouses their hostility.

Because of their exceptionally swift and skillful flight, the adult kites have few natural enemies, but the eggs or nestlings are vulnerable to such enemies as crows, jays, the larger hawks and owls, and to certain mammalian predators, notably raccoons. Also, many nests probably are destroyed by the sudden and violent summer storms that are characteristic of the High Plains. Bendire (1892: 178) cited observations by Goss that in a hailstorm in Barber County, Kansas, eggs were destroyed in many kites' nests and some of the nests were almost completely demolished. Several nests found by me to have incubating eggs in the first week of June were abandoned or had disappeared completely by July 18, but the cause was not evident. One nest that was under observation on July 22 had nestlings approximately two-thirds grown on that date, but on August 4 only a few sticks remained, and the carcass of a fledgling dangled from a limb ten feet below the nest. Even at the Park where firearms are prohibited, kites are sometimes shot by ignorant or malicious persons. In general, Kansas ranchers recognize the harmless and beneficial habits of kites, appreciate their esthetic appeal and protect them, but many persons use them as convenient targets, with utter disregard for the Federal laws protecting them. Because of the strong popular prejudice against raptorial birds in general, laws protecting them are usually not enforced. Law enforcement officers do not take action even when clear-cut violations come to their attention. Arrest and prosecution for the killing of any kind of raptor is almost out of the question in Kansas.

Ratio of Immatures to Adults

In the juvenal plumage flight feathers of the kites are brown, barred with white, much different in appearance from the dark, slaty plumage of adults. Bent (*op. cit.*:67) stated that these barred flight feathers are retained through the second summer, and he quoted Mr. G. W. Stevens as having found kites breeding in this immature plumage. On June 2, 1961, I attempted to determine the ratio of these yearling kites to others in the population at the

Park. Most of the kites seen were in flight too far away to discern definitely whether or not they were juveniles, and records were limited to those seen at relatively close range. In a total of 108 records only 11 pertained to these yearlings and the remaining 97 were identified as of adults. Beyond doubt in the course of my counts some individuals were recorded repeatedly, therefore the counts are not entirely acceptable. However, on each occasion that kites were seen in numbers in early summer, the adults greatly outnumbered the juveniles. The approximate nine to one ratio of adults to yearlings seems much too high. Even if the difference is much less than indicated, the high ratio of adults to yearlings would seem to imply that the adults have a long life expectancy. A rather improbable alternative is that some of the yearlings remain in winter quarters or wander elsewhere rather than accompanying the adults on the return migration to their breeding grounds. Still another alternative is that the breeding season of 1960 was relatively unsuccessful, but this idea is negated by my own observations at the Park in late 1960, as recently fledged young were numerous then.

At the time of my visit to the Park August 21 to 24, 1961, all young had recently left the nests and were able to fly. However, their behavior was so much different from that of the adults that a reliable ratio could not be obtained. The fledglings tended to remain in the nest tree, or to make relatively short flights near it, while the adults occupied with catching of prey for themselves and their young, spent much of their time aloft. The adults were hence far more conspicuous than the fledglings. However, it is my impression that the fledglings were from one-third to one-fourth as numerous as the adults. If this ratio is correct, and if all adults had bred, from two-thirds to three-fourths of the eggs and/or nestlings must have been destroyed. This rate of loss seems reasonable in view of the known histories of nests observed in June and again in July, and of the fates of birds' nests in general.

Summary

Mississippi kites were studied in southwestern Kansas in the summer of 1961, at various localities, especially at Meade State Park. At this locality, near the northwestern limit of the breeding range, the kite thrives in typical High Plains habitat dominated by a short-grass type of vegetation, but availability of trees suitable for nests is a limiting factor. Since maturing of extensive groves of cottonwoods and other trees planted at Meade State Park, the

colony of kites has increased tremendously and the breeding population probably exceeded 100 in 1961.

The kites are social in all their activities and do not maintain territories. The sexes differ little in appearance, but males are slightly smaller than females and have paler heads. Food consists almost entirely of flying insects, and these are usually eaten while the kite is in flight. Kites that are feeding nestlings may travel up to two miles from the nest or perhaps considerably farther in the course of their foraging. For 148 feedings of nestlings the observed intervals averaged 10.7 minutes. Most published references to the food habits mention predation on small vertebrates, especially lizards, but including also snakes, toads, rodents, and even rabbits. In my study a total of 205 pellets were collected and 453 insects were tentatively identified but the total number of insects in the pellets was much larger. No vertebrates were identified from this sample and among 358 prey items identified from kite stomachs collected in Oklahoma, by Sutton, vertebrae of a small fish were the only vertebrate remains. Further verification of predation on mammals, reptiles and amphibians by this species is needed. Of the insects distinguished in pellets, beetles including carabids, cicindelids, hydrophilids, scarabaeids, and silphids were most numerous (270) and grasshoppers (164) were second; also there were 16 cicadas and three moths.

Kites arrive in Kansas about the second week in May. Often old nests are repaired and used over again. Hatching is about mid-June. Normally there are two eggs per clutch. By mid-August the fledglings are learning to fly. By the latter part of August they are learning to capture their insect prey, and in early September southward movement of the entire population begins.

Eggs and/or young in many nests are destroyed by hail or high wind in the sudden violent storms that are characteristic of the High Plains. Mississippi kites are often shot by misguided persons, and benefit little from the protection supposedly provided by Federal law. However, the adults probably have few natural enemies. The high ratio of older adults to yearlings indicates that the life expectancy is long. Through their second summer the kites retain their barred immature plumage, and can be readily distinguished from adults. Only ten per cent of the kites recorded in 108 June sight records at the Park were in juvenile plumage.

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Jaw Musculature Of the Mourning and White-winged Doves

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Jaw Musculature Of the Mourning and White-winged Doves

BY

ROBERT L. MERZ

For some time many investigators have thought that the genus *Zenaida,* which includes the White-winged and Zenaida doves, and the genus *Zenaidura,* which includes the Mourning, Eared, and Socorro doves (Peters, 1937:83-88), are closely related, perhaps more closely than is indicated by separating the several species into two genera. It is the purpose of this paper to report investigations on the musculature of the jaw of doves with the hope that, together with the results of other studies, the relationships of the genera *Zenaida* and *Zenaidura* can be elucidated.

METHODS AND MATERIALS

In order to determine in each species the normal pattern of musculature of the jaws, heads of 13 specimens of doves were dissected (all material is in the Museum of Natural History of The University of Kansas): White-winged Doves (*Zenaida asiatica*), 40323, 40324, 40328, 40392, 40393; Zenaida Doves (*Z. aurita*), 40399, 40400; Mourning Doves (*Zenaidura macroura*), 40326, 40394, 40395, 40396, 40397, 40398.

Thirty-seven skulls from the collection of the Museum of Natural History of The University of Kansas and two skulls from the United States National Museum were measured. The measurements are on file in the Library of The University of Kansas in a dissertation deposited there by me in 1963 in partial fulfillment of requirements for the degree of Master of Arts in Zoology. Specimens used were: White-winged Doves, KU 19141, 19142, 19143, 19144, 19145, 19146, 19147, 23138, 23139, 24337, 24339, 24341, 23592, 23593, 24340, 31025, 31276; Mourning Doves, KU 14018, 14781, 15347, 15533, 15547, 15550, 15662, 15778, 15872, 16466, 17782, 17786, 17788, 17795, 19153, 19242, 20321, 21669, 22394, 22715; Eared Doves (*Zenaidura auriculata*), USNM 227496, 318381. Additionally, the skulls of the Zenaida Doves mentioned above were measured. All measurements were made with a dial caliper and read to tenths of a millimeter.

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I would like also to acknowledge the assistance of Dr. Robert M. Mengel and Mr. Jon C. Barlow for suggestions on procedure, and Mr. William C. Stanley, who contributed specimens of Mourning Doves for study. Mr. Thomas

H. Swearingen offered considerable advice on production of drawings and Professor E. Raymond Hall suggested the proper layout of the same and gave editorial assistance otherwise, as also did Professor Johnston.

MYOLOGY

The jaw musculature of doves is not an imposing system. The eating habits impose no considerable stress on the muscles; the mandibles are not used for crushing seeds, spearing, drilling, gaping, or probing as are the mandibles of many other kinds of birds. Doves use their mandibles to procure loose seeds and grains, which constitute the major part of their diet (Leopold, 1943; Kiel and Harris, 1956: 377; Knappen, 1938; Jackson, 1941), and to gather twigs for construction of nests. Both activities require but limited gripping action of mandibles. The crushing habit of a bird such as the Hawfinch (*Coccothraustes coccothraustes*), on the other hand, involves extremely powerful gripping (see, for example, Sims, 1955); the contrast is apparent in the development of the jaw musculature in the two types. Consequently, it is not surprising to find a relatively weak muscle mass in the jaw of doves, and because the musculature is weak there are few pronounced osseous fossae, cristae and tubercles. As a result, the bones, in addition to being small in absolute size, are relatively weaker when compared to skulls of birds having more distinctive feeding habits which require more powerful musculature.

The jaw muscles of the species dissected for this study are, in gross form, nearly identical from one species to another. Thus, a description of the pertinent myology of each species is unnecessary; one basic description is hereby furnished, with remarks on the variability observed between the species.

The terminology adopted by me for the jaw musculature is in boldfaced italic type. Synonyms are in italic type and are the names most often used by several other writers.

M. pterygoideus ventralis: part of Mm. pterygoidei, Gadow, 1891:323-325, table 26, figs. 1, 2, 3 and 4, and table 27, fig. 3—part of M. pterygoideus internus, Shufeldt, 1890:20, figs. 3, 5, 6, 7 and 11—part of M. adductor mandibulae internus, Edgeworth, 1935:58, figs. 605c and 607—part of M. pterygoideus anterior, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. pterygoideus dorsalis: part of Mm. pterygoidei, Gadow, 1891:323-325, table 26, fig. 7 and table 27, figs. 1 and 3—part of M. pterygoideus internus, Shufeldt, 1890:20—part of M. adductor mandibulae internus, Edgeworth, 1935:58, fig. 605c—? part of M. pterygoideus anterior, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. adductor mandibulae externus: a) pars superficialis: parts 1 and 2 of M. temporalis, Gadow, 1891:320-321—part of M. temporal, Shufeldt, 1890:16, figs. 5 and 7—part of M. adductor mandibulae externus, Edge-

worth, 1935:58-60—M. capiti-mandibularis medius and profundus, Adams, 1919:101, pl. 8, fig. 1.

b) *pars medialis:* ? parts 1, 2 and 3 of M. temporalis, Gadow, 1891:320-322—part of M. masseter and ? part of M. temporal, Shufeldt, 1890: 16-18, figs. 5, 6, 7 and 11—part of M. adductor mandibulae externus, Edgeworth, 1935:58-60—M. capiti-mandibularis superficialis, first part, Adams, 1919:100-101, pl. 8, fig. 1.

c) *pars profundus:* part 2 of M. temporalis, Gadow, 1891:321, table 27, fig. 2—part of M. temporal and ? part of M. masseter, Shufeldt, 1890: 16-18—part of M. adductor mandibulae externus, Edgeworth, 1935: 58-60—? part of M. capiti-mandibularis medius and all of pars superficialis, second part, Adams, 1919:100-101.

M. pseudotemporalis profundus: M. quadrato-maxillaris, Gadow, 1891: 322-323—M. pterygoideus externus, Shufeldt, 1890:20-21, figs. 3, 5 and 11—part of M. adductor mandibulae medius, Edgeworth, 1935:58-59—? part of M. pterygoideus posterior, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. protractor pterygoidei: part 4b of M. temporalis, Gadow, 1891: 322-323, table 27, fig. 4—part of M. entotympanious, Shufeldt, 1890:19-20, figs. 3 and 11—part of M. spheno-pterygo-quadratus, Edgeworth, 1935: 57.

M. depressor mandibulae: M. digastricus s. depressor mandibulae, Gadow, 1891:318-319—M. biventer maxillae, Shufeldt, 1890:18-19, figs. 3, 4, 5, 6, 7 and 11.

M. pseudotemporalis superficialis: M. spheno-maxillaris, Gadow, 1891:323—part of M. temporal, Shufeldt, 1890:16—part of M. pseudotemporalis, Hofer, 1950:468-477—part of M. adductor mandibulae medius, Edgeworth, 1935:277.

M. adductor mandibulae posterior: ? part of M. temporal, Shufeldt, 1890: 16—part of M. adductor mandibulae medius, Edgeworth, 1935:58-59—? part of M. pterygoideus posterior, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. protractor quadrati: part 4a of M. temporalis, Gadow, 1891:322-323, table 27, fig. 4—part of M. entotympanicus, Shufeldt, 1890:19-20, figs. 3 and 11—part of M. spheno-pterygo-quadratus, Edgeworth, 1935:57.

The terminology adopted by me is that of Lakjar (1926) except that the divisions of *M. depressor mandibulae* are designated by the Latinized equivalents of the names used by Rooth (1953:261-262).

M. pterygoideus ventralis lateralis.—The origin is fleshy and by aponeurosis on the ventral side of the palatine anterior to the palatine fossa. The insertion is fleshy on the ventromedial surface of the lower mandible and continues along the anteromedial surface of the internal angular process to its distal tip. A few fibers leave *pars lateralis* and insert on an aponeurosis which receives also all the fibers of *M. pterygoideus dorsalis lateralis.* The latter fact may have prompted Rooth (1953:257) to make the statement that the fibers originating on the dorsal part of the palatine inserted more laterally than those originating on the ventral side. Rooth worked with *Columba palumbus,* the Woodpigeon, and his description concerned *M. adductor mandibulae internus pterygoideus,* which is composed of *Mm. pterygoideus ventralis et dorsalis* of Lakjar (1926). His assertion that ventral fibers, that is to say, fibers arising on the ventral surface of the palatine, insert medially does not appear to be completely true for doves.

Aponeuroses cover most of the lower surface of the muscle and one or two nerves extend into the substance of the muscle. The nerves run from the

anterior edge of *M. pterygoideus dorsalis medialis* and farther posteriorly from a separation in the muscle.

M. pterygoideus ventralis medialis.—The origin is by aponeurosis from the ventral surface of the palatine and fleshy from the palatine fossa. The aponeurosis is the same that gives origin to the fibers of *pars lateralis*. Part of the aponeurosis becomes tendonlike in the middle of *M. pterygoideus ventralis* and separates its two divisions. The insertion is fleshy on the lower one-third of the anterior surface of the internal angular process of the lower mandible, and by two tendons on the distal tip of that process. Many of the fibers of *pars medialis* insert on the tendons. The fibers at their insertion are not distinctly separate from those of *pars lateralis* and there is considerable mingling of the fibers. Consequently, the medial part of *M. pterygoideus ventralis* cannot be removed as a part distinct from the lateral part (figs. 1, 4, 10, 21 and 22).

Ordinarily *M. pterygoideus ventralis* does not cross the ventral edge of the lower mandible, but in one white-wing the muscle was slightly expanded on the right side and it could be seen in lateral view. The homologous muscle in *Columba palumbus* apparently is consistently visible in lateral view. (See Rooth, 1953, fig. 6.)

M. pterygoideus dorsalis medialis.—The origin is fleshy on the dorsolateral surface of the palatine immediately anterior to the pterygoid and also on the anterior, dorsolateral, posterior and ventromedial surfaces of the pterygoid. The insertion is fleshy on the ventromedial surface of the lower mandible and the anterior surface of the internal angular process immediately dorsal to the insertion of *M. pterygoideus ventralis lateralis*.

M. pterygoideus dorsalis lateralis.—The origin is fleshy from the dorsolateral surface of the palatine, anterior to the origin of *pars medialis* and the insertion is by means of an aponeurosis on the medial surface of the lower mandible, lateral to the insertion of *M. pterygoideus ventralis lateralis*. The aponeurosis crosses the medial side of the insertion of *M. pterygoideus dorsalis medialis*. The fibers run in a posteroventrolateral direction and insert on the ventromedial side of the aponeurosis (figs. 1, 6, 8, 9, 13-22).

In one individual, a Mourning Dove, the origin of *pars lateralis* of *M. pterygoideus dorsalis* extended to the pterygoid. With this one exception the muscle was uniform throughout the several species.

M. adductor mandibulae externus.—This is the most complex muscle in the jaw owing to its system of tendons and aponeuroses. Three divisions of this muscle were described by Lakjar (1926:45-46) and the divisions appear to be distinguishable in the doves, but there is no clear line of demarcation for any of the parts and the following description is based upon my own attempts to delineate the muscle.

M. adductor mandibulae externus superficialis.—The origin is fleshy from the most lateral area of the temporal fossa. Dorsally the origin is bounded by the base of the postorbital process and ventrally by the temporal process. The fibers converge upon a tendon that passes beneath the postorbital ligament and runs anteriorly among the fibers of *pars profundus*. The insertion is tendinous on the dorsal surface of the lower mandible in common with the dorsal aponeurosis of *pars profundus*. The insertion is immediately anterior

to the ventral aponeurosis of *pars profundus* near the medial edge of the dorsal surface on a tubercle at the posterior end of the dorsal ridge of the lower mandible.

M. adductor mandibulae externus medialis.—The origin is by a flat, heavy tendon from the temporal process. The tendon is attached almost vertically on the temporal process. It twists approximately 130° as it runs anteriorly, and becomes a thin aponeurosis, which gives rise on its dorsal and ventral surfaces to many fibers that insert in a fan-shaped area on the mandibular fossa. Fibers from the dorsal and dorsomedial sides of the heavy tendon run rostrad and insert on the ventral surface of the dorsal aponeurosis of *pars profundus*. From the ventral surface the most posterior fibers converge on an aponeurosis that inserts on a transverse crista on the dorsal surface of the mandible immediately lateral to the ventral aponeurosis of *pars profundus* and dorsal to the insertion of *M. adductor mandibulae posterior*. The more anterior fibers insert fleshily on the mandibular fossa. The tendon of origin is actually one with the ventral aponeurosis of *pars profundus*, which is situated in a horizontal plane. The insertion is primarily a fleshy attachment on the mandibular fossa. Some of the fibers that arise on the dorsomedial and lateral surfaces of the tendon of origin attach to another tendon, which inserts in the midline of the mandibular fossa on a small tubercle near the anterior end. Also, there is insertion by an aponeurosis anterior to *M. adductor mandibular posterior* as stated above. Fibers attach to the dorsal and ventral side of the aponeurosis.

M. adductor mandibulae externus profundus.—The origin is fleshy from the medial surface of the temporal fossa, the posterior wall of the orbit and the otic process of the quadrate. The origin is bounded laterally by the origin of *pars superficialis* and medially by the origin of *M. pseudotemporalis superficialis*. Ventrally the muscle lies against its own ventral aponeurosis, which originates on the posterior wall of the orbit immediately above the articulation of the otic process of the quadrate, and which also receives many fibers from the surface of the quadrate. The insertion is primarily by means of two aponeuroses. The most dorsal aponeurosis inserts on a tubercle at the posterior tip of the dorsal edge of the mandible. The lateral tendon of *M. pseudotemporalis superficialis* converges with the aponeurosis. It is superficial and there are no fibers on its dorsal surface. The ventral aponeurosis inserts on a crista immediately below the insertion of the dorsal aponeurosis. It receives fibers on its ventral surface from the otic process of the quadrate, and on its dorsal surface gives rise to fibers that insert on the dorsal aponeurosis (figs. 2, 3, 5, 9, 10, 11, 13-18).

The tendon of insertion of *pars medialis* of *M. adductor mandibulae externus* does not become a superficial aponeurosis posteriorly in the Zenaida Dove as it does in the Mourning and White-winged doves.

M. pseudotemporalis profundus.—The origin is fleshy from the medial and partially from the dorsal surface of the lower mandible. The origin is almost completely anterior to and partly dorsal and ventral to the medial (most anterior) insertion of *M. pseudotemporalis superficialis*. The anterior margin of the origin is at the point where the mandibular ramus of the trigeminal nerve enters the mandible. Posteriorly the origin is bounded by the insertion

of *M. adductor mandibulae posterior,* and ventrally by a ridge that is situated about halfway down the medial side of the mandible. The insertion is by aponeurosis on the tip of the orbital process of the quadrate and fleshily on the anterior surface of the same process. The aponeurosis extends about three-fifths of the distance along the muscle and it is dorsal or superficial to all of the fibers. Many fibers insert on the ventral side of the aponeurosis (figs. 1, 5, 13, 14, 15, 16, 21 and 22).

This muscle is the most variable of all the jaw muscles. In the Mourning Dove the muscle appears rather slender in dorsal view and in the White-winged Dove has an enlarged lateral belly that gives the appearance of a thicker muscle. In the Zenaida Dove *M. pseudotemporalis profundus* is intermediate in shape between those of the other two species. This muscle will be discussed in detail later.

M. protractor pterygoidei.—The origin is fleshy from the junction of the sphenoidal rostrum and the interorbital septum. Fibers converge on the pterygoid in anteroventrolateral and posteroventrolateral directions. The posterior edge of the muscle is in contact with *M. protractor quadrati* with which its fibers mingle. The insertion is fleshy on the posterior surface of the lateral half of the pterygoid to its articulation with the body of the quadrate (figs. 6, 8, 9, 11, 13-20).

M. depressor mandibulae superficialis medialis.—The origin is fleshy from the lateral edge of the basioccipital where the muscle is attached to *Ligamentum depressor mandibulae* and extends in a lateral direction to a point where the structures involved turn dorsad. The insertion is by fibers and a light aponeurosis on the crista that is situated on the posteroventromedial edge of the lower mandible.

M. depressor mandibulae superficialis lateralis.—The origin is fleshy from the squamosal region, slightly posteroventral to the origin of *M. adductor mandibulae externus superficialis.* A thin aponeurosis lies medial to the muscle fibers. The insertion is by means of an aponeurosis that becomes tendonlike along the posteroventrolateral crista and the posteriormost part of the ventral edge of the lower mandible.

M. depressor mandibulae medialis.—The origin is fleshy from the lateral and ventral surfaces of *Ligamentum depressor mandibulae.* The insertion is fleshy on the posterior surface of the lower mandible, posterodorsal to the insertions of *partes superficialis medialis et lateralis* (figs. 4, 9, 10, 13 and 14).

The parts of *M. depressor mandibulae* are difficult to distinguish from one another because of considerable intermingling of fibers.

M. pseudotemporalis superficialis.—The origin is fleshy from the posterior wall of the orbit, dorsal to the foramen of the trigeminal nerve, lateral to the origin of *M. protractor quadrati* and medial to *M. adductor mandibulae externus profundus.* The insertion is by means of an aponeurosis that bifurcates at the point of contact with the mandibular ramus of the trigeminal nerve, which is at the level of the orbital process of the quadrate (except in the Mourning Dove where the division is more anterior), and which inserts as two tendons on the dorsomedial edge of the lower mandible posterior to the insertion of *M. pseudotemporalis profundus.* The lateral tendon is superficial to the dorsomedial edge of *M. adductor mandibulae externus,* and converges with the aponeurosis of *pars profundus* of that muscle and inserts with it on

a tubercle near the dorsomedial edge of the mandible anterior to the insertion of *M. adductor mandibulae posterior* as mentioned before. The anterior half of the medial tendon lies ventral to the lateral edge of *M. pseudotemporalis profundus* and the mandibular ramus of the trigeminal nerve. All of the fibers of the muscle insert on the posteroventral surface of the aponeurosis before it divides. Part of *M. pseudotemporalis profundus* also lies ventral to the medial tendon of *M. pseudotemporalis superficialis* and, in effect, the tendon is imbedded in the substance of *M. pseudotemporalis profundus* as it proceeds anteriorly. The trigeminal nerve leaves a slight impression on the ventral surface of the muscle near its origin (figs. 1, 3, 11, 13, 14, 15 and 16).

M. adductor mandibulae posterior.—The origin is fleshy from the anterodorsal and anterior surfaces of the quadrate body, from the anterodorsolateral, medial and anterior surfaces of the orbital process of the quadrate. The muscle also has an origin from the otic process of the quadrate, partly fleshy and partly by a slight aponeurosis. The insertion is fleshy on the dorsal and lateral surfaces of the mandible immediately anterior to the articulating surface. This muscle also has extensive insertion on the medial side of the lower mandible dorsal to the insertion of *M. pterygoideus dorsalis medialis* and posterior to the origin of *M. pseudotemporalis profundus* (figs. 1, 3, 5, 17, 18, 19 and 20).

The fibers of *M. pseudotemporalis profundus* can be distinguished from the fibers of *M. adductor mandibulae posterior* because the pterygoideus nerve passes between the two (Lakjar, 1926:55). Rooth (1953:255-256) considers as part of this muscle the ventral aponeurosis of *pars profundus* of *M. adductor mandibulae externus* and all the fibers ventral to it. But I could not justify the inclusion of that aponeurosis as part of *M. adductor mandibulae posterior* in the doves because none of the fibers of *M. adductor mandibulae posterior* as I have described it were attached to that particular aponeurosis.

M. protractor quadrati.—The origin is fleshy from the posterior wall of the orbit medial to the foramen of the trigeminal nerve and also medial to the origin of *M. pseudotemporalis superficialis*. The origin describes an arc in the horizontal plane until it reaches the interorbital septum and the optic nerve. The insertion is fleshy on the posteromedial edge of the body of the quadrate and the orbital process of the quadrate and on the otic process of the quadrate. The muscle also inserts on the ventromedial surface of the orbital process of the quadrate and the adjacent area of the body of the quadrate (figs. 5, 7, 9, 11, 13-18).

M. protractor quadrati possesses many fibers that arise from *M. protractor pterygoidei*. Consequently, it is difficult to determine the exact extent of the origin or the insertion of either muscle.

ACTION OF JAW MUSCLES

M. pterygoideus ventralis.—Contraction of this muscle retracts the upper mandible by moving the palatine posteriorly, and simultaneously adducts the lower mandible.

M. pterygoideus dorsalis.—This muscle functions in essentially the same manner as *M. pterygoideus ventralis*. The result of having a part of its origin on the pterygoid as well as on the palatine is to facilitate retraction of the upper mandible.

M. adductor mandibulae.—This is the chief adductor of the lower mandible and the muscle functions solely in that capacity. In birds having great crushing ability, this muscle is much larger and more powerful and the skull is reinforced behind the quadrate in order to withstand the pressure of the lower mandible against the quadrate during adduction (Sims, 1955:374 and Bowman, 1961:219-222).

M. pseudotemporalis profundus.—With origin and insertion on highly movable bones, this muscle, when it contracts, retracts the upper mandible and adducts the lower mandible. Like the pterygoid muscles, this muscle, by itself, would allow the bird to grasp objects by means of its mandibles. However, *M. pseudotemporalis profundus* could produce a more powerful grip because it takes origin farther anteriorly on the lower mandible.

M. protractor pterygoidei.—Contraction of *M. protractor pterygoidei* pulls the pterygoid anteromedially and causes it to slide forward along the sphenoidal rostrum. This action aids in protraction of the upper mandible.

M. depressor mandibulae.—The depressor of the lower mandible is the sole muscle other than *M. geniohyoideus* involved in the function of abducting the lower jaw of doves. Its size can be correlated especially well with feeding habits of the bird. Other birds that force their closed mandibles into fruit, wood or the earth and then forcibly open them, belong to groups possessing enlarged depressors. Contraction of the muscle pulls the postarticular (retroarticular) process upward with the resultant downward movement of that part of the mandible which is anterior to the articulation. Since there is no "gaping" in doves the muscle is only large enough to overcome the inherent tone of the relaxed adductor muscles.

In some non-passerine species as well as in certain passerines the muscle also serves to raise the upper jaw by acting on the quadrate, which is capable of rotating vertically on its otic process. Especially in the gapers, where resistance is offered near the tip of the lower mandible, contraction of the muscle pulls the entire mandible dorsad thus forcing the jugal and palatal struts forward (Zusi, 1959:537-539). The action supplements that of *Mm. protractor pterygoidei et quadrati* and is enhanced by anterior migration of the origin of *M. depressor mandibulae.*

There is no lifting action involved in contraction of the depressor muscle in doves for two reasons—(A) the origin of the muscle is situated much too far posteriorly on the skull, and, more important, (B) the quadrate is not hinged for vertical movement. As will be discussed later, it moves only in a horizontal plane.

M. pseudotemporalis superficialis.—Like *M. adductor mandibulae,* this muscle performs only the one function of adducting the lower mandible, and like *M. pseudotemporalis profundus* it is a synergist of that muscle.

M. adductor mandibulae posterior.—Although this muscle undoubtedly acts as an adductor of the lower mandible, I believe that, because of its disadvantageous insertion so near the articulation, its main function must be concerned with firming the mandible against the quadrate. This is to say that its function is partially that of a ligament.

M. protractor quadrati.—When *M. protractor quadrati* contracts, the quadrate bone is swung medially. This action, as mentioned previously, results in

protraction of the upper jaw, and, as a consequence, its action supplements the action of *M. protractor pterygoidei.*

CRANIAL OSTEOLOGY

The ability of most birds to protract the upper mandible, and the structure of the skull which enables them to do so are responsible for common reference to the skull as "kinetic" (Beecher, 1951a:412; Fisher, 1955:175). The movement is effected by muscular action on a series of movable bones that exert their forward force on the upper mandible, which in turn swings on a horizontal hinge, the "naso-frontal hinge," at the base of the beak. The bone initiating the movement is the quadrate, which is hinged posteriorly by its otic process and which ordinarily swings up or down depending on the muscle or muscles being contracted at any given moment. The upward swing of the quadrate pushes the jugal bar, which is attached to its lateral tip, along its longitudinal axis, in an anterodorsal direction, and the force is transferred to the upper mandible, which is thereby elevated. A synergetic mechanism is simultaneously initiated by the same bone—the quadrate. Since the quadrate body articulates with the pterygoid, the upward movement forces the pterygoid to slide along a ridge in the ventral midline of the cranium, the sphenoidal rostrum, thus pushing the palatine forward and exerting an upward push on the upper mandible.

In the columbids the quadrate has a bifurcated otic process that functions as the hinge. The posterior tips of the forks are situated almost vertically (one above the other) and the movement of the quadrate is not so much up and down, or vertical, as it is horizontal (fig. 12). When the quadrate moves medially the upper mandible is protracted; a lateral movement results in retraction. There is a slight, almost negligible, upward movement of the quadrate. The movements of the various bony elements were observed on a skull that had been made flexible by boiling in water for a minute as suggested by Beecher (1951a:412).

Also in the columbids the naso-frontal hinge is not constructed in the same manner as it is in many other birds as there is not a simple hinge across the entire base of the beak. In fact, there is no true hinge at all in the area of the nasals, but those bones are extremely thin and they bend or flex under pressure. Actually, the hinge is double or divided. One part is on either side of the nasals. The hinges are situated at the posterodorsal tips of two thin processes of the maxillary bones and the appearance is not unlike that of half a span of a suspension bridge having the hinges

at the tops of the towers. Several other species of birds share this type of hinge construction with columbids.

The movement of the lower jaw is, of course, the primary operation involved in opening the mouth. The lower jaw possesses a deep fossa at its posterior end, or on its posterodorsal surface, which articulates with the body of the quadrate bone. The length of that part of the mandible extending behind the articulation is directly correlated with the resistance offered the mandible in opening, since it is on the posterior extension that the depressor of the lower mandible inserts. The larger the muscle the more surface is needed for attachment. Also the added length of the mandible posterior to the articulation serves as a lever in opening the mandible, and the fulcrum is moved relatively farther forward.

In birds lacking resistance to abduction of the lower mandible, as in doves, it is nevertheless necessary for a slight postarticular process to remain for the insertion of a small depressor muscle which, as mentioned previously, is necessary to counteract the relaxed adductor muscles of the lower jaw.

There are many exceptions to the rule that birds have kinetic skulls, and usually a secondary fusion and reinforcement of bones around the hinge has limited or eliminated all movement. Sims (1955) describes the Hawfinch's immobile upper jaw, which is used as a powerful press in cracking the stones of fresh fruit. Skulls of woodpeckers have been modified somewhat in the same manner as a result of their foraging and nesting habits (Burt, 1930).

The two most distantly related members of the genera under investigation are the White-winged Dove, *Zenaida asiatica*, and the Mourning Dove, *Zenaidura macroura*. They were chosen to demonstrate differences and likenesses in proportions of members of the genera.

Ten measurements were taken on each skull, but simple observation reveals that, in relation to total length of the skull, the beak of the White-winged Dove is longer than that of the Mourning Dove. Tip of upper mandible to base of beak averaged 48.6 and 42.9 per cent of the total length of the skull in the White-winged Dove and Mourning Dove, respectively. The position of the jugal bar has remained about the same with respect to the cranial part of the skull, and the entire cranial part of the skull is almost the same shape in the species studied.

Likewise, in the White-winged Dove the distance from the anterior tip of the lower mandible to the anterior part of *M. adduc-*

tor mandibulae externus is relatively longer in relation to the length of the lower mandible than in the Mourning Dove. Finally, the position of the jugal with respect to the naso-frontal hinge is about the same in the two species.

Measurements and calculations indicate that the longer beak of the White-winged Dove as compared with the Mourning Dove is a function of the beak itself, not of differences in other parts of the skull. Measurements of skulls of Eared and Zenaida doves support this view.

OTHER MORPHOLOGICAL FEATURES

In the species dissected, the only variable muscle that I consider significant in revealing relationships is *M. pseudotemporalis profundus.* It is markedly enlarged in the White-winged Dove in relation to the homologous muscle in the Mourning Dove. The muscle is enlarged in such a manner that a lateral expansion of its mass is apparent in superficial or dorsal view (compare figures 15 and 16). This, of course, indicates a muscle with powerful contraction, which has been unable to enlarge its circumference symmetrically because the eye is immediately dorsal to the muscle. Therefore it has expanded laterally. Ventral expansion is blocked by the presence of other muscles, and medially there is no surface for the insertion of additional fibers on the orbital process of the quadrate.

The jaw musculature has been known for some time to be highly adaptive (Beecher, 1951a and b, 1953; Bowman, 1961; Burt, 1930; Engels, 1940 and Goodman and Fisher, 1962) and it would not be unreasonable, I think, to expect the jaw muscles of closely related species with similar habits to be similar. The beak of the White-winged Dove is longer in proportion to the length and height of the skull (exclusive of the beak) than is the beak of the Mourning Dove. The lengthened beak is probably an adaptation for nectar-feeding, which has been documented by McGregor, Alcorn and Olin (1962:263-264) while investigating pollinating agents of the Saguaro Cactus (*Cereus giganteus*), and by Gilman (1911:53) who observed the birds thrusting their bills into the flowers of the plant. Gilman indicated, however, that he could not be sure if the birds were seeking insects, pollen, or nectar. In any event the lengthened bill probably facilitates getting food by birds that probe parts of flowers. Hensley (1954:202) noted that both Mourning and White-winged doves were "exceptionally fond of

this source of nourishment." But he also points out an "interesting correlation" between the presence of the white-wings in the desert and the flowering of the saguaro. During his studies the appearance of the first white-wing preceded the opening of the first saguaro flower by two days. The flowering and fruiting season lasted until August, the month of termination of the white-wing breeding season.

Since Hensley makes the correlation solely with the white-wings, I assume that there is no other obvious correlation between plants and birds among the remainder of the avifauna of the desert. Probably the Mourning Dove has failed to adapt to nectar-feeding as yet, and the White-winged Dove is the primary exploiter of this food niche. It should be noted, also, that the head of the Mourning Dove is smaller than the white-wing's, and perhaps there is no need for an elongated beak for reaching deeply into the flowers.

The lengthened bill should produce no difficulties in protraction of the upper mandible and depression of the lower for the reason that in the dove there is no known resistance offered to these movements. The genus *Icterus* furnishes an example wherein resistance is met in the process of opening the mandibles; individuals of this genus thrust their closed bill into certain fruits and forcibly open their mandibles against the resistance of the pulp by strong protraction and depression, thus permitting the juices of the fruit to lake and ultimately to be consumed (Beecher, 1950:53). Beecher refers to the technique used in fruit-eating as "gaping." The result of gaping in *Icterus* should be the presence of a more massive set of muscles concerned with protraction and depression than is found in non-gaping groups. Beecher found the situation to be exactly as expected in that genus and in other genera which also gape. Meadowlarks (*Sturnella*) and caciques (*Archiplanus*) gape and pry in soil and wood respectively (Beecher, 1951a:422 and 426).

The lengthened beak would be a problem when the White-winged Dove attempted to pick up objects such as seeds, which do in fact constitute the largest percentage of its diet in spite of its nectar-feeding habit. A similar situation exists in the genus *Icterus*, which is primarily adapted for gaping even though it shows a preference for insects when they are abundant (Beecher, 1950:53). The lengthened beak could be compensated for by (A) migration of the anterior end of the jugal bar toward the rostral tip of the bill and away from the fronto-nasal hinge with a simultaneous enlargement of the adductor muscles of the lower mandible, or

(B) enlargement of the one muscle that functions simultaneously as an efficient retractor of the upper mandible and adductor of the lower mandible, namely *M. pseudotemporalis profundus*. *Mm. pterygoideus dorsalis et lateralis* perform the same function, but because of their position on the lower mandible they, apparently, are stronger retractors of the upper mandible than they are adductors of the lower.

It will be recalled that the jugal bar bears the same, or nearly the same, relationship to the cranium in the white-wing as it does in the Mourning Dove and that the heads, excluding the beaks of both species, are of nearly the same proportions. Also, *Mm. adductor mandibulae externus* and *pseudotemporalis superficialis*, the chief adductor muscles of the lower mandible, were not noticeably enlarged in the white-wing. It is also important to note that other combinations of migration of bone and/or enlargement of muscles could successfully solve the problem of providing sufficient leverage for the proper functioning of the lengthened mandibles, but it is my thesis that the second alternative sufficed for seed-eating habits and that that is the adaptation that was established; it is, in fact, the only one present in the White-winged Dove.

It is unlikely that this enlarged muscle and beak are the remains of another series of jaw muscles that have converged toward the condition in Mourning Doves. Columbids are almost unquestionably monophyletic, and two lines would have had to diverge and then converge. There is no evidence for such an evolutionary occurrence.

GENERIC RELATIONSHIP

An attempt will be made here to summarize all the available evidence, direct or indirect, which bears on the problem of relationship of these genera. The original dissections which are discussed in this report are only valuable as one more bit of evidence concerning one characteristic that aids in clarification of generic relationship, and it is only in conjunction with other evidence that any satisfactory conclusion may be forthcoming.

Morphology

My dissections demonstrated that, in relation to the size of the doves, the jaw musculature of all the specimens investigated was so nearly alike that only one major difference was detected. *M. pseudotemporalis profundus* appeared to be enlarged in the White-winged Dove. This might have been predicted, since the white-

wing was also shown to possess an elongated beak, presumably an adaptation for nectar-feeding, which would necessitate additional muscle development in order to compensate for the added length. Measurements recorded from several skulls indicated that the heads of the birds (excluding the beak) are nearly proportional.

Perhaps plumage patterns are the most widely used characters for determining generic relationships of birds. Ridgway (1916: 339-385) followed the columbid classification of Salvadori (1893) using plumage patterns and body proportions to distinguish between the genera. In the genus *Zenaidura* he included the unique specimen *Zenaidura yucatanensis,* and he placed *auriculata* in *Zenaida.* The White-winged Dove was referred to a separate genus, *Melopelia.* He described the genus *Zenaidura* in the following manner:

"Plumage of head, neck and under parts soft and blended; bare orbital space moderate, broadest beneath eyes. Coloration plain, the proximal secondaries (sometimes adjacent wing-coverts and scapulars also) spotted with black; rectrices (except middle pair) with a black band across postmedian portion, the apical portion paler gray than basal portion, sometimes white; a small black subauricular spot; adult males with head, neck and anterior under parts more or less vinaceous and sides of neck glossed with metallic purple."

He noted that the plumage of *Zenaida* was almost precisely as described for *Zenaidura.* Also, although all members of *Zenaida* reputedly possessed twelve rectrices, a characteristic of the genus, it was later found that *auriculata* possessed fourteen rectrices. The species was promptly placed in the genus *Zenaidura* by Peters (1934:213-215). In plumage and coloration, *Melopia* was described as similar to *Zenaida* and *Zenaidura* but without black spots on the wings.

The White-winged Dove also has twelve rectrices, but Bond (1940:53) and Goodwin (1958:330-334) considered the number and shape of rectrices to be of minor importance when compared to the homologous markings of the plumage. Goodwin stated that his conclusion was emphasized by the fact that the tail of *auriculata* is intermediate in length and shape between those of *macroura* and *aurita.* In summary Goodwin "lumped" the genera *Zenaida* and *Zenaidura* under the genus *Zenaida.*

Nidification

It has been adequately documented that members of these genera closely resemble one another in their nesting and egg-laying habits. Bent (1932:407, 417), Davie (1889:157), Goss (1891:242)

and Nice (1922:466) have described the two, white eggs of the clutch of the Mourning Dove. They have also noted that their nests are composed mainly of twigs and may be constructed in trees, shrubs or on the ground. The Eared Dove has nearly identical habits (Bond, 1961:104), and a similar situation exists with the Zenaida Dove (Audubon, 1834:356; Bent, 1932:418-419).

Like the other species, White-winged Doves lay two white or buffy eggs per clutch and build frail nests of sticks (Bent, 1932: 431; Wetmore, 1920:141; Baird, Brewer and Ridgway, 1905:377).

The point to be made here is simply this: If the species in question are to be considered congeneric then it might reasonably be expected that they would display some similarity in nidification and egg-laying. If their habits varied considerably it would not necessarily mean that their relationship was more distant, but similarities can usually be considered indicative of affinities because they are the phenotypic expression of the partially unaltered genotype of the common ancestor.

Interbreeding

Intergeneric crosses of columbids in captivity are common, but in nature there is little evidence that even interspecific crosses occur. Only one apparent hybrid between members of the genus *Zenaida* and genus *Zenaidura* has ever been discovered. The individual was taken on the Yucatan peninsula of Mexico, and was described and named as a new species (*Zenaidura yucatanensis*).

Salvadori (1893:373), Ridgway (1916:353) and Peters (1934: 213-215) agree that *Zenaidura yucatanensis* Lawrence is a hybrid between *Zenaidura macroura marginella* and *Zenaida aurita yucatanensis*. Ridgway (1916:355), however, notes that ". . . If *Zenaidura yucatanensis* Lawrence should prove to be really a distinct species, and not a hybrid . . . unquestionably *Zenaida* and *Zenaidura* can not be separated generically, since the former is in every way exactly intermediate between the two groups." In the event that the unique type is a hybrid, the very fact of its existence supports the hypothesis that the genera are more closely related than is currently recognized.

Serology

There have been no investigations having as their sole purpose the clarification of the relationship of the genera *Zenaida* and *Zenaidura*. But some work has involved the comparison of the antigenic content of individual columbids with the antigenic content of a member of another species of the same family.

Irwin and Miller (1961) tested, along with other columbids, members of *Zenaida* and *Zenaidura* for presence of, 1) species-specific antigens of *Columba guinea* (in relation to *Columba livia*) which are designated A, B, C and E, and, 2) species-specific antigens of *C. livia* (in relation to *C. guinea*) which are designated A′, B′, C′ and E′.

In the first test all five species of *Zenaida* and *Zenaidura* possessed antigens A and C, and all but *auriculata* possessed E. None of the species gave evidence of the presence of the B antigen of *C. guinea* in their blood. In the latter test only *macroura* had A′, only *asiatica* had B′ (*aurita* was not tested for B′), and none had C′ or E′.

These results would indicate that the five species are similar regarding antigenic content of the blood, and the variation is not consistent within one or the other genus as presently known.

SUMMARY AND CONCLUSION

The avian genus *Zenaida* is currently considered to be distinct from the genus *Zenaidura* by most columbid taxonomists. The jaw muscles of six Mourning Doves (*Zenaidura*) and five White-winged Doves (*Zenaida*) were investigated as to differences and similarities that might clarify the relationships of the genera. The sizes and proportions of skulls were also considered in 37 Mourning and White-winged doves and two Eared Doves. Larger size of *M. pseudotemporalis profundus,* the muscle that functions simultaneously as an adductor of the lower jaw and retractor of the upper jaw, in the White-winged Dove was the character found in the jaw musculature that could be used to support the contention that *Zenaidura* and *Zenaida* represent distinct genera. Larger size of this muscle in the white-wing seems to be related to its elongated beak. The long beak apparently is used for nectar-feeding in flowers of the Saguaro Cactus.

Excluding the beak, skulls of the white-wing and Mourning doves are of nearly the same shape. Previous investigators have shown that in *Zenaida* and *Zenaidura* plumage patterns are similar, nesting habits and eggs are nearly identical, blood proteins are similar, and one "intergeneric" hybridization in nature is known.

Consequently, it is concluded that species of the two alleged genera are congeneric, and I agree with Goodwin (1958) that the genus *Zenaida* (Bonaparte, 1838:41) should include the Mourning Dove, Eared Dove, Socorro Dove, Zenaida Dove, and White-winged

Dove. Their Latin binomina are *Zenaida macroura, Zenaida auriculata, Zenaida graysoni, Zenaida aurita,* and *Zenaida asiatica,* respectively.

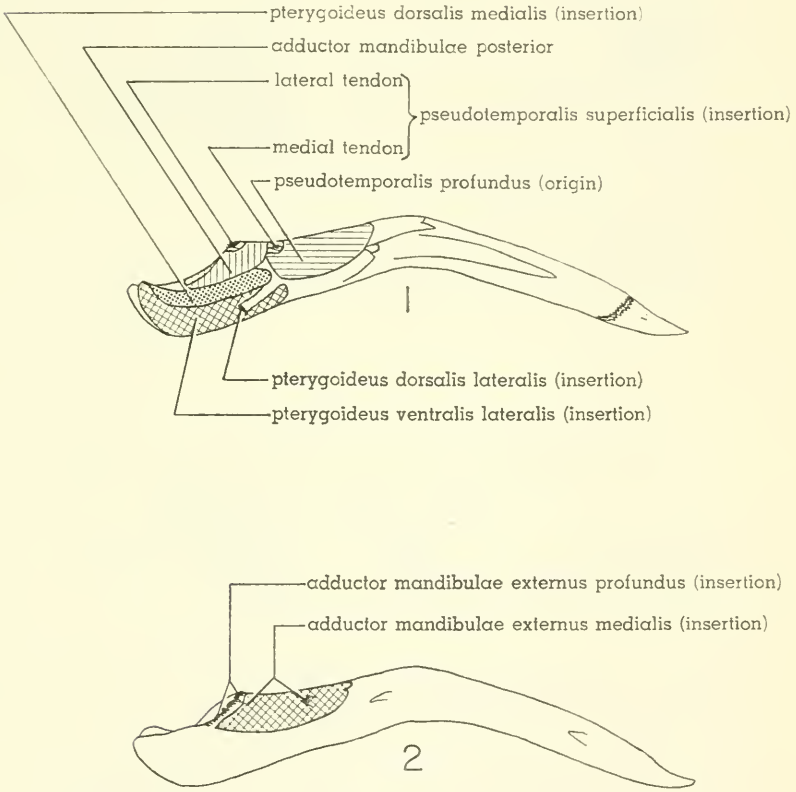
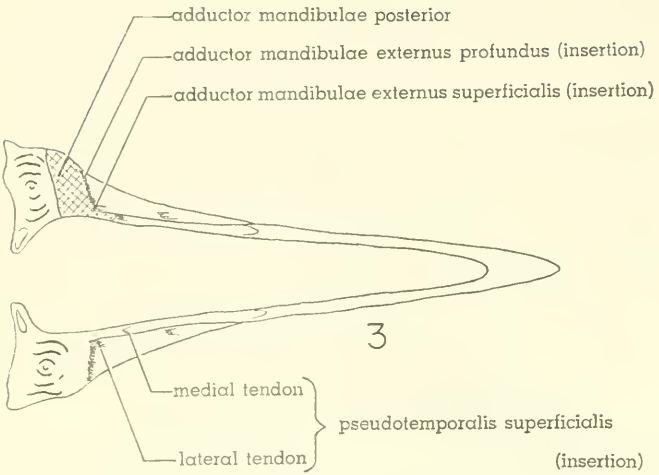


FIG. 1. Medial view of left ramus of lower mandible of Mourning Dove. × 2½.

FIG. 2. Lateral view of right ramus of lower mandible of Mourning Dove. × 2½.



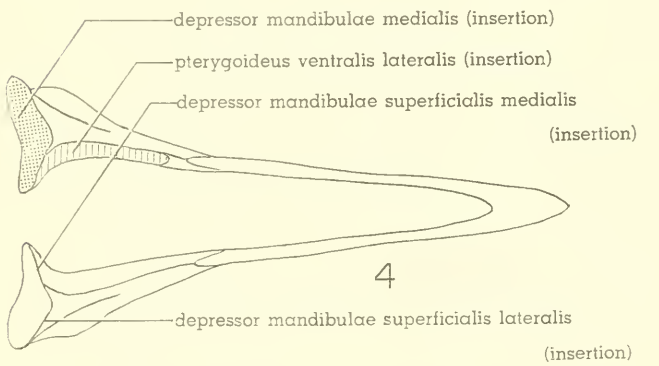
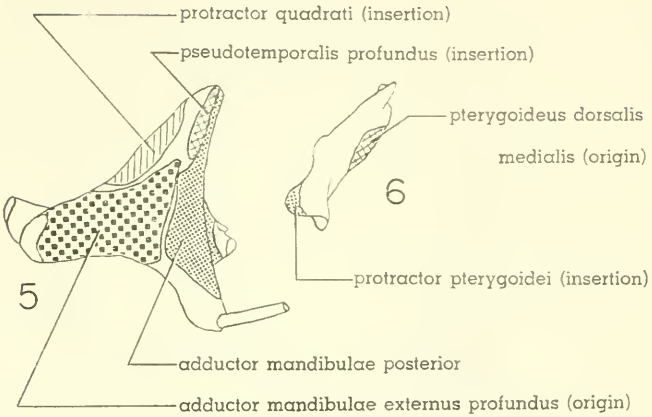


FIG. 3. Dorsal view of lower mandible of Mourning Dove. × 2½.

FIG. 4. Ventral view of lower mandible of Mourning Dove. × 2½.



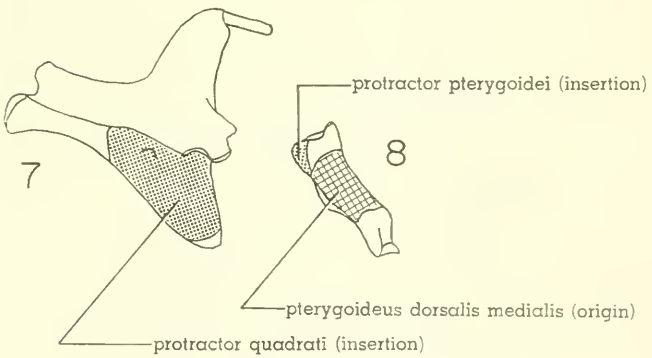


FIG. 5. Dorsal view of right quadrate of Mourning Dove. × 5.
FIG. 6. Dorsal view of right pterygoid of Mourning Dove. × 5.
FIG. 7. Ventral view of right quadrate of Mourning Dove. × 5.
FIG. 8. Ventral view of right pterygoid of Mourning Dove. × 5.

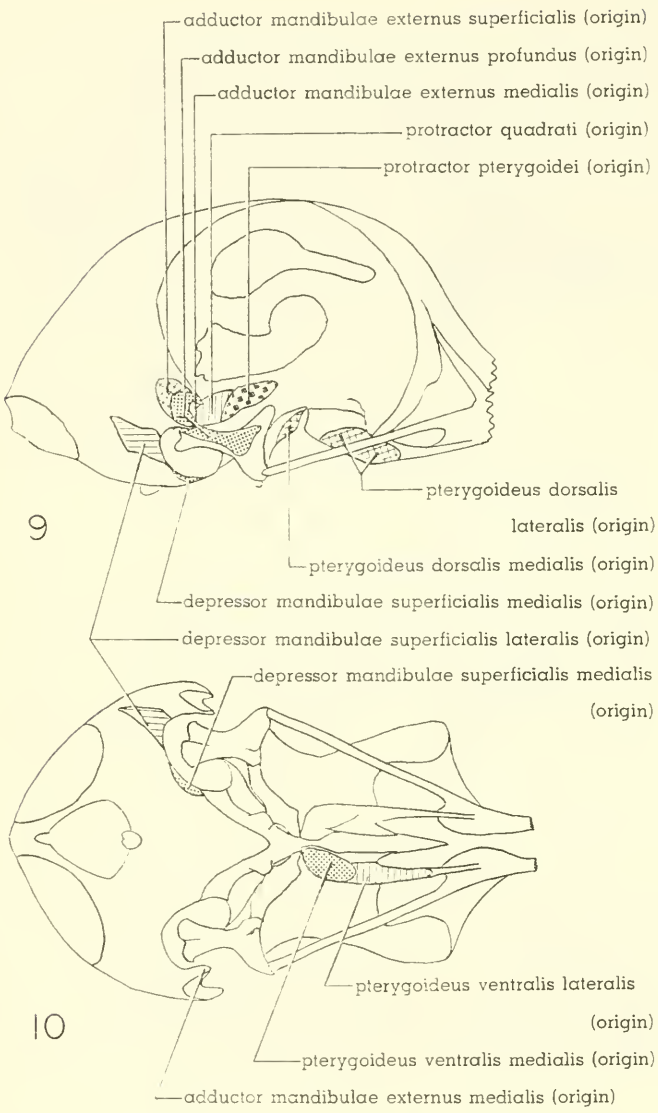
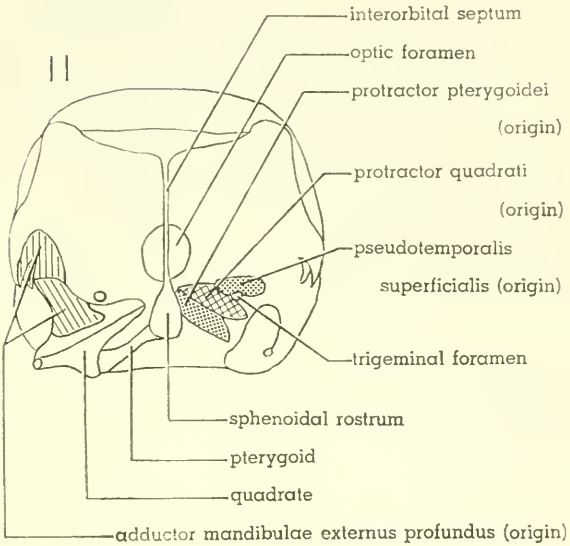


FIG. 9. Right lateral view of skull of Mourning Dove. × 2½.

FIG. 10. Ventral view of skull of Mourning Dove. × 2½.



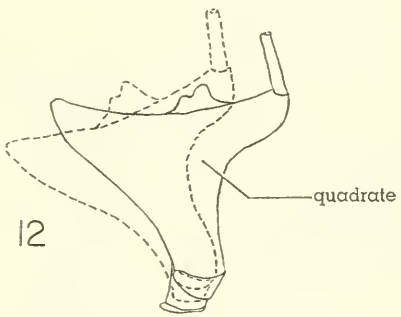


FIG. 11. Cross section of skull of Mourning Dove; anterior view. × 2½.

FIG. 12. Dorsal view of right quadrate of Mourning Dove showing movement which protracts the upper mandible (broken line). × 5.

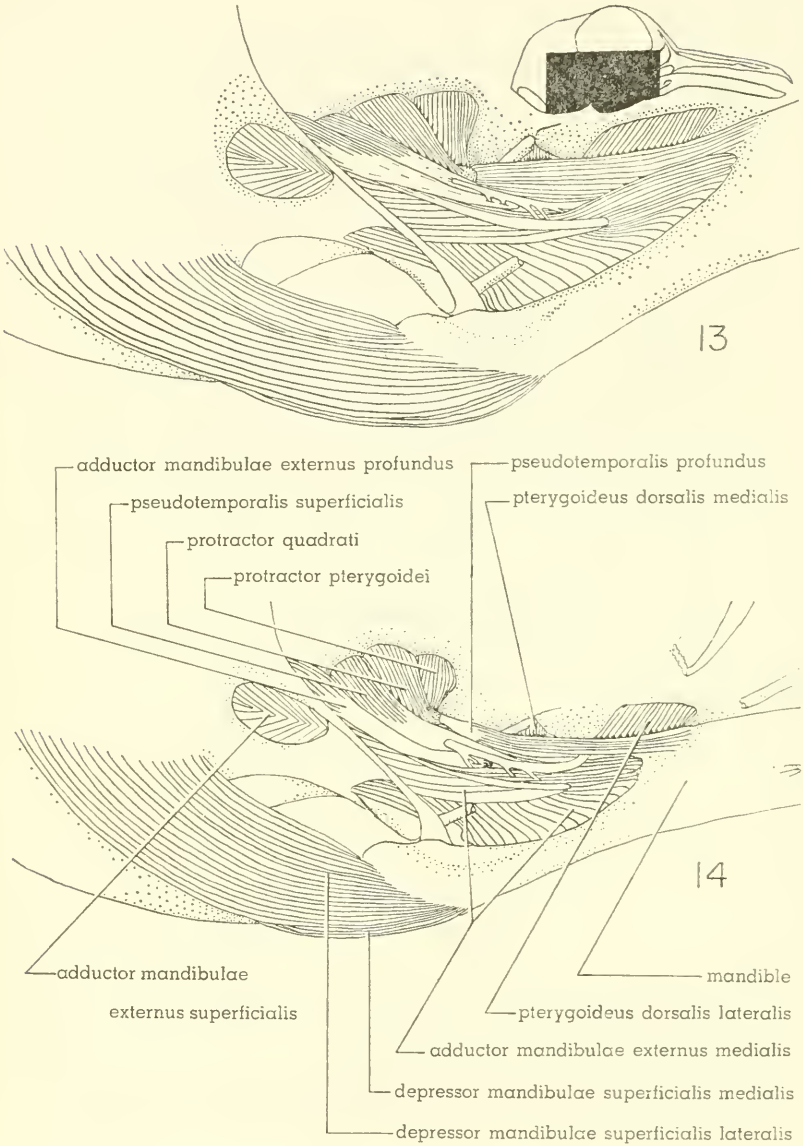
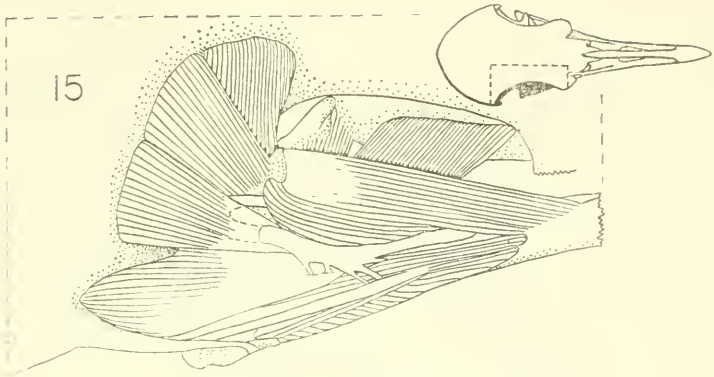


FIG. 13. Right lateral view of the jaw musculature of the White-winged Dove; superficial layer. × 5.

FIG. 14. Right lateral view of the jaw musculature of the Mourning Dove; superficial layer. × 5.



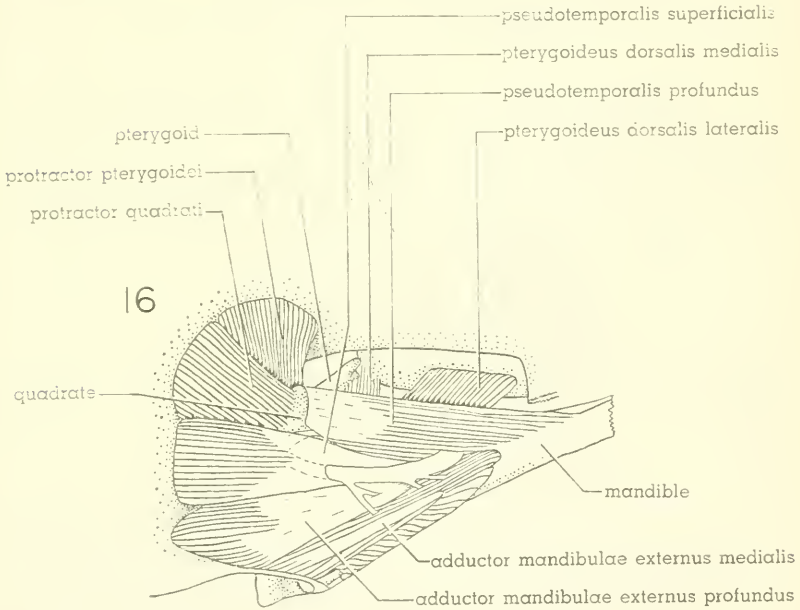
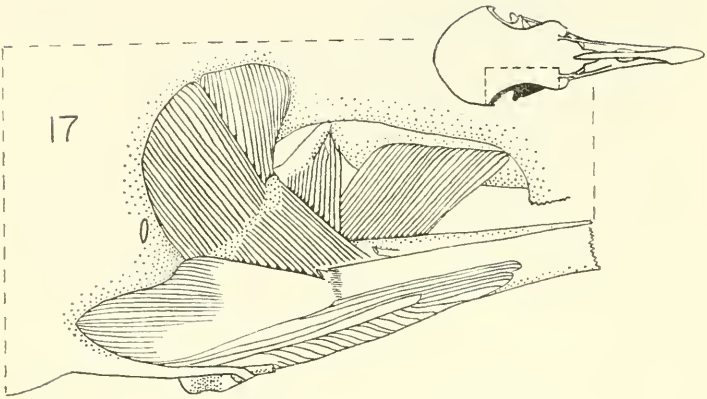


FIG. 15. Dorsal view of the jaw musculature of the White-winged Dove (right side); superficial layer. × 5.

FIG. 16. Dorsal view of the jaw musculature of the Mourning Dove (right side); superficial layer. × 5.



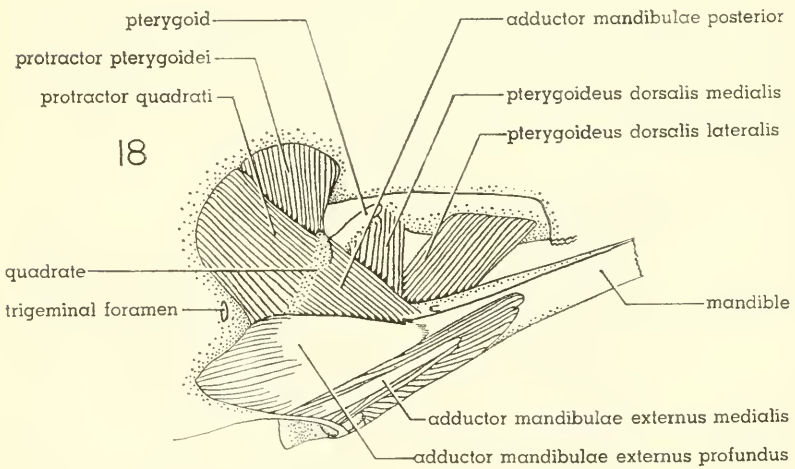
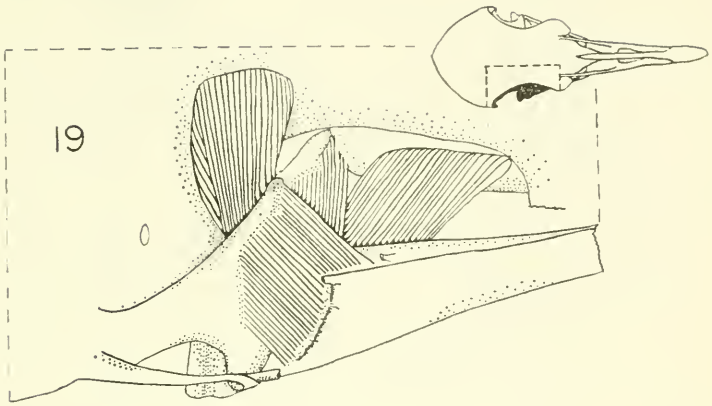


FIG. 17. Dorsal view of the jaw musculature of the White-winged Dove (right side); middle layer. × 5.

FIG. 18. Dorsal view of the jaw musculature of the Mourning Dove (right side); middle layer. × 5.



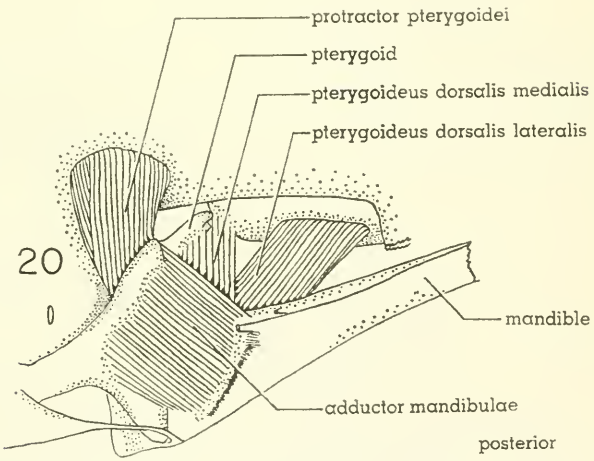


FIG. 19. Dorsal view of the jaw musculature of the White-winged Dove (right side); deep layer. × 5.

FIG. 20. Dorsal view of the jaw musculature of the Morning Dove (right side); deep layer. × 5.

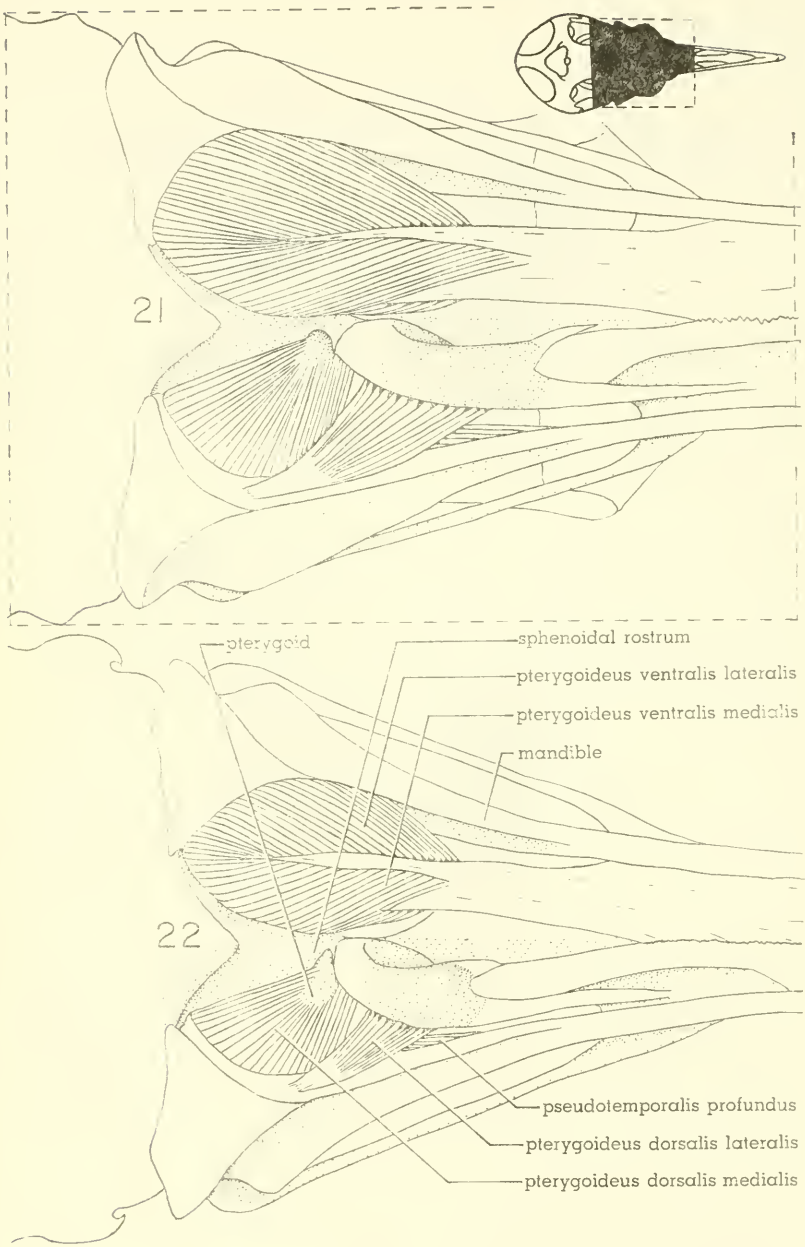


FIG. 21. Ventral view of the jaw musculature of the White-winged Dove (*M. depressor mandibulae* not shown). × 5.

FIG. 22. Ventral view of the jaw musculature of the Mourning Dove (*M. depressor mandibulae* not shown). × 5.

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Thoracic and Coracoid Arteries In Two Families of Birds, Columbidae and Hirundinidae

BY

MARION ANNE JENKINSON

University of Kansas
Lawrence
1964

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INTRODUCTION

Most descriptions of the circulatory system of birds, largely the work of Glenny, have dealt with arteries of the neck and thorax in a wide variety of species. As a result of his work, Glenny offered several hypotheses concerning the phylogenetic, hence taxonomic, significance of differences in some of these vessels. He also described six types of thoracic arterial arrangements and stated that these categories might represent various levels of evolution (Glenny, 1955:543-544).

The families Columbidae (pigeons) and Hirundinidae (swallows) have two nearly extreme arterial types described by Glenny, and are universally acknowledged as monophyletic. Differences within the families, therefore, can be considered as valid intrafamilial differences. I have investigated the thoracic and coracoid arteries and their branches in members of these two families to determine the degree of individual variability of the vessels, and the possible causes of interspecific and intrafamilial differences.

METHODS AND MATERIALS

All specimens studied are in The University of Kansas Museum of Natural History. They were preserved in alcohol and their blood vessels were not injected. Dissections were made with the aid of a binocular microscope at magnifications of 10 × and 20 ×.

Following is a list of the species studied, the number of individuals of each species dissected, and the catalogue numbers of the specimens. The nomenclature and classification are those of the American Ornithologists' Union's *Check-List of North American Birds*, fifth edition (1957).

Family Columbidae

Zenaidura macroura (Linnaeus), Mourning Dove 2: 40325, 40326.
Zenaida asiatica (Linnaeus), White-winged Dove 1: 40328.
Scardafella inca (Lesson), Inca Dove 5: 34894, 34896, 34902, 34906, 34907.
Columba livia Gmelin, Rock Dove (domestic pigeon) 1: 40321.

Family Hirundinidae

Iridoprocne bicolor (Vieillot), Tree Swallow 1: 38101.
Progne subis (Linnaeus), Purple Martin 5: 37711, 38794, 38796, 38798, 38804.
Stelgidopteryx ruficollis (Vieillot), Rough-winged Swallow 1: 38277.
Riparia riparia (Linnaeus), Bank Swallow 2: 38784, 38785.
Hirundo rustica Linnaeus, Barn Swallow 1: 38839.

The following descriptions are of *Progne subis* and *Scardafella inca*. Differences in the vascular system in other members of the families represented by *P. subis* and *S. inca* are mentioned at the appropriate places. The muscles briefly described for each of these two species are those that are supplied by the thoracic or coracoid arteries or by branches of the same, and muscles that, by their origin, location, or insertion, seem to affect the course or origin of one of these arteries.

The following sources have been particularly useful for the terminology of muscles and of skeletal features: Ashley (1941), Beddard (1898), Coues (1903), Howard (1929), Howell (1937), and Hudson and Lanzillotti (1955).

The names used for most arteries are those in common usage for vertebrates. I have not used the terms "internal mammary" and "intercostal" artery as substitutes for "thoracic" artery, except when referring to the work of others. The vessel's homology with the internal mammary artery of mammals has been denied (Glenny, 1955:541), and the name "mammary" is certainly not useful descriptively in birds. The term "intercostal" is less objectionable, except that such a name may call to mind segmental vessels arising from the dorsal aorta. The term "thoracic" seems best, as it is reasonably descriptive, and has been used by Glenny in the majority of his descriptions covering a wide variety of birds. The name "sternoclavicular" has been used by others as a synonym for the "coracoid" artery. I have arbitrarily chosen to use the latter.

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MYOLOGY AND ANGIOLOGY: HIRUNDINIDAE

Figs. 1, 2, 3, and 4 illustrate the following muscles and arteries described for *Progne subis.*

Myology

M. pectoralis thoracica, Fig. 1. The origin is from slightly less than the posterior half of the sternum, from the ventral half of the keel, almost the entire length of the posterolateral surface of the clavicle and adjacent portion of the sterno-coraco-clavicular membrane, and tendinously from the ventral thoracic ribs. This massive muscle covers the entire ventral surface of the thorax and converges to insert on the ventral side of the humerus on the pectoral surface.

M. supracoracoideus, Fig. 1. The origin is from the dorsal portion of the keel and medial portion of the sternum, and is bordered ventrally by the origin of *M. pectoralis thoracica,* and laterally by *M. coracobrachialis posterior.* The origin is also from the manubrium and the anterolateral portion of the proximal half of the coracoid and to a slight extent from the sterno-coraco-clavicular membrane adjacent to the manubrium. This large pinnate muscle converges, passes through the foramen triosseum, and inserts by a tendon on the external tuberosity of the humerus, immediately proximal to the insertion of *M. pectoralis thoracica.*

M. coracobrachialis posterior, Figs. 1 and 3. The origin is from the dorsolateral half of the coracoid, anterolateral portion of the sternum (where the area of origin is bordered medially by *M. supracoracoideus,* posteriorly by *M. pectoralis thoracica,* and laterally by *M. sternocoracoideus*), and also to a slight extent from the area of attachment of the thoracic ribs to the sternum. The muscle fibers converge along the lateral edge of the coracoid and insert on the median crest of the humerus immediately proximal to the pneumatic foramen. In passing from the origin on the sternum to the insertion on the humerus, the belly of the muscle bridges the angle formed by the costal process of the sternum and the coracoid.

M. sternocoracoideus, Figs. 2 and 3. The origin is from the entire external surface of the costal process of the sternum, and to a small extent from the extreme proximal ends of the thoracic ribs where they articulate with the costal process. The muscle inserts on a triangular area on the dorsomedial surface of the coracoid. Like *M. coracobrachialis posterior,* this muscle bridges the angle formed by the costal process and the coracoid.

M. subcoracoideus (ventral head), Figs. 2 and 3. The origin is from the dorsomedial edge of the coracoid at its extreme proximal end, and to a slight extent from the adjacent portion of the manubrium. The origin is medial to the insertion of *M. sternocoracoideus.* The ventral head passes anterodorsally along the medial edge of the coracoid and joins the dorsal head (not here described). The combined muscle then inserts by a tendon onto the internal tuberosity of the humerus.

M. costi-sternalis, Figs. 1, 2, and 3. The origin is from the anterior edge of the sternal portion of the first four thoracic ribs. This triangular muscle narrows and inserts on the posterior edge of the apex of the costal process. The portion arising from the first rib may share slips with *M. sternocoracoideus.*

M. costi-sternalis anterior, Figs. 1, 2, and 3. This muscle is variously developed, and originates from a small area on the ventral end of the vertebral portion of the last cervical rib. The insertion is on the apex of the costal process, immediately anterior to the insertion of *M. costi-sternalis.*

Mm. intercostales externus, Fig. 1. These muscles extend posteroventrally between the vertebral portions of successive thoracic ribs, and between the last cervical and first thoracic ribs. In the more posterior intercostal spaces these muscles are poorly developed, but they become progressively better developed anteriorly, and are fully represented in the most anterior intercostal spaces.

Mm. intercostales internus, Fig. 3. These muscles resemble the external intercostal muscles, but extend anteroventrally, with the muscles being most fully developed posteriorly, and progressively less so anteriorly.

Costopulmonary muscles, Fig. 3. This diagonal series of muscle slips from the thoracic ribs attaches to the aponeurosis covering the lungs.

Angiology

Figs. 3 and 4 show all arteries discussed for this family. The numbers following the names or descriptions of arteries in the text refer to numbered arteries in one or both of these figures.

The right and left innominate or brachiocephalic arteries arise from the aortic trunk and give rise to the common carotid arteries (14). The major vessel continuing across the thoracic cavity is the subclavian artery. Classically the subclavian is considered as continuing into the anterior appendage as the axillary artery. However, in the species studied, the axillary artery can best be described as a branch from the subclavian; the pectoral stem forms a more direct continuation of the subclavian. In traversing the thoracic cavity, the subclavian gives rise to the thoracic, coracoid, and axillary arteries, and leaves the thoracic cavity as the pectoral trunk, dorsal to the area where *Mm. coracobrachialis posterior* and *sternocoracoideus* span the agle formed by the coracoid and costal process.

The pectoral trunk bifurcates into two main pectoral arteries (9), which penetrate *M. pectoralis thoracica.* Neither the axillary artery nor these pectoral arteries were traced in my study.

The coracoid artery (2) arises from the ventral face of the subclavian (1), either opposite the base of, or medial to, the axillary artery (10). The coracoid artery passes ventrad between the medial edge of the coracoid and the ventral head of *M. subcoracoideus,* and an artery (7) is given off to supply that muscle. The main vessel then penetrates *M. supracoracoideus* and bifurcates or ramifies into several vessels (12).

Between the origin of the coracoid artery from the subclavian, and the point where the coracoid artery passes the medial edge of the coracoid, several branches are given off. These vessels are highly variable in origin, as described below, and not all were always found. Along with the coracoid artery, they are termed a "coracoid complex."

The first artery (11) of this complex arises from any one of several places: from the lateral face of the coracoid artery at its base; independently from the subclavian immediately lateral to the origin of the coracoid artery; and from the thoracic artery near its origin. This vessel travels laterad, parallel to the

subclavian, and penetrates *M. coracobrachialis posterior* at the same point that the pectoral artery passes dorsal to that muscle.

Another vessel (common stem of 4 and 5) of the coracoid complex in most specimens arises from the anterior face of the coracoid artery and branches into several vessels, some of which (5) supply *M. subcoracoideus*, and some of which (4) feed *M. coracobrachialis posterior*. The vessel occasionally shares a common stem with the main vessel (11) to *M. coracobrachialis posterior*, and in some specimens arises independently from the subclavian, immediately anterior to the origin of the coracoid artery. The branch (4) to *M. coracobrachialis posterior* was also seen to arise independently from any of the above-mentioned positions.

Two remaining vessels (6 and 8) are often found as branches from the coracoid artery. They were small and often were collapsed in the individuals I dissected, but were most clearly seen in *Iridoprocne bicolor*. The vessels occasionally had a common base, and in some specimens only one vessel was found. The first artery (6) passes mediad into *M. sternocoracoideus*, or continues across that muscle onto the inner face of the sternum. The second vessel (8) also supplies *M. sternocoracoideus* or the inner surface of the sternum, and often a large branch continues across the dorsal surface of the coracoid to *M. coracobrachialis posterior*. Fig. 3 shows a composite of these vessels; not all branches were seen in any one specimen. In the specimen of *I. bicolor* a foramen existed on the lateral edge of the coracoid where the branch (of 8) to *M. coracobrachialis posterior* passed. An examination of skeletons of five to 10 individuals each of the five species for which dissections were made, and of *Petrochelidon pyrrhonota* (Cliff Swallow) and *Tachycineta thalassina* (Violet-green Swallow), in the University of Kansas collection, showed that most coracoids of these seven species of swallows had a small notch (as shown in Fig. 4) or a complete foramen there.

The thoracic artery (3) arises from the subclavian opposite the base of the coracoid artery, or from the base of the coracoid artery. Of the five specimens of *P. subis* dissected, one individual had the former arrangement on both sides, and one had the latter on both sides, whereas in the remaining three the thoracic artery arose from the coracoid artery on one side and from the subclavian on the other side. The distance between these two possible sites of origin is slight.

The thoracic artery usually passes ventral to *M. costi-sternalis anterior*. Occasionally a small artery (13) could be traced from the main trunk of the thoracic artery to that muscle. The main thoracic artery bifurcates near the insertion of *M. costi-sternalis*, the branches traveling posteriad on both sides of the muscle. On one side of one specimen this artery bifurcated immediately after leaving the subclavian, the dorsal trunk passing dorsal to *M. costi-sternalis anterior*, and the ventral trunk ventral to the muscle. On the other side of the same individual the artery passed dorsal to *M. costi-sternalis anterior*, bifurcating at the normal point.

From the ventral trunk of the thoracic artery a variable number of small vessels arises to supply the costosternal articulations. The main ventral trunk bifurcates into two branches, one of which passes onto the inner face of the sternum, and one of which supplies the posterior two intercostal spaces.

The dorsal thoracic trunk supplies *M. costi-sternalis*, several dorsal intercostal areas, and the costopulmonary muscles. Minor variations in all of the smaller branches of the thoracic artery were common.

MYOLOGY AND ANGIOLOGY: COLUMBIDAE

Figs. 5, 6, and 7 illustrate the following muscles and arteries described for *Scardafella inca.*

Myology

M. pectoralis thoracica, Fig. 5. The origin is from approximately the ventral third of the keel, the lateral and anterior portion of the clavicle and the adjacent sterno-coraco-clavicular membrane, and from the lateral portion of the sternum and the fascia overlying the thoracic ribs. This massive muscle covers the entire ventral surface of the thorax, converges, and inserts on the pectoral surface on the ventral side of the humerus.

M. supracoracoideus, Fig. 5. The origin is from the dorsal two-thirds of the keel and medial half of the sternum (where the origin is bordered ventrally, posteriorly, and laterally by the origin of *M. pectoralis thoracica*) and from the sterno-coraco-clavicular membrane adjacent to the coracoid. This large pinnate muscle converges, passes through the foramen triosseum, and inserts by means of a strong tendon on the dorsal surface of the humerus on the deltoid ridge.

M. coracobrachialis posterior, Fig. 5. The origin is from a prominent lateral wing on the posterolateral portion of the coracoid, and from the lateral surface of the proximal two-thirds of the coracoid. The insertion is by means of a tendon on the internal tuberosity of the humerus. Of the musles described here, this one differs most strikingly from the homologous muscle in *P. subis.* The difference can be seen by comparing Figs. 1 and 5.

M. sternocoracoideus, Figs. 5, 6, and 7. The origin is from the external, and to a slight extent from the internal, surface of the costal process. The insertion is on a posterolateral triangular area on the dorsal surface of the coracoid.

M. costi-sternalis, Figs. 5 and 6. The origin is from the anterior edge of the sternal portion of the first three thoracic ribs. The muscle converges and inserts on the apex of the costal process.

M. subcoracoideus (ventral head), Fig. 6. The origin is from the manubrium and from approximately the posterior half of the coracoid and on the medial and dorsal surface of that bone, and the medial side of the sterno-coraco-clavicular membrane adjacent to the coracoid. The ventral head passes anterodorsally to join with the dorsal head (not here described), and the combined muscle inserts by a tendon on the internal tuberosity of the humerus.

Mm. intercostales externus, Fig. 5. These muscles extend posteroventrally between successive thoracic ribs and between the last cervical and first thoracic ribs.

Mm. intercostales internus, Fig. 7. These muscles extend anteroventrally between the last three thoracic ribs.

Costopulmonary muscles, Fig. 7. This series of muscle slips from the thoracic ribs attaches to the aponeurosis covering the lungs.

Angiology

Figs. 5, 6, and 7 show all arteries discussed for this family. The numbers following names or descriptions of arteries in the text refer to numbered arteries

in one of these figures. Insofar as possible, the numbers used for these arteries are the same numbers used for the homologous vessels in swallows.

The right and left innominate arteries arise from the aortic trunk and give rise to the common carotid (14) and subclavian (1) arteries. The latter continues across the thoracic cavity, giving rise to the coracoid (2) and axillary (10) arteries, and becoming the pectoral trunk. That trunk swings posteriorly and leaves the thoracic cavity near the apex of the costal process, as shown in Fig. 7. Where the trunk passes under *M. sternocoracoideus,* the thoracic artery (3) is given off.

The various branches of the coracoid artery, again referred to as a "coracoid complex," are as follows: The first branch, from the posterior face of the coracoid artery, is a relatively large vessel (6) here termed the sternal artery; it passes mediad across *M. sternocoracoideus,* sending off a branch (6a) to that muscle. The right sternal artery continues posteriorly on the midline of the inner surface of the sternum, and appears to send branches into the various pneumatic foramina of the sternum, but these vessels are minute and exceedingly difficult to trace accurately. The corresponding left vessel is smaller and ramifies on the anteromedial surface of the sternum. Variations found in these vessels were the following: In one specimen of *S. inca* the sternal artery had, on both sides, an independent origin from the subclavian, lateral to the origin of the coracoid artery. In *Zenaidura macroura* both right and left sternal arteries were similar to the left vessel described above, no median longitudinal vessel being seen. In *Columba livia* no vessel corresponding to the sternal artery was seen. In *Zenaida asiatica* these arteries penetrated *M. sternocoracoideus;* no branch to the sternum was seen.

A small complex of vessels (4 and 4a) arises from the lateral face of the coracoid artery and feeds *M. coracobrachialis posterior,* and occasionally *M. sternocoracoideus.* One branch (4a) passes under the coracoid and travels along the lateral side of that bone, supplying small branches to *M. coracobrachialis posterior,* and finally ramifying on the head of the coracoid. In *C. livia, Zenaidura macroura,* and *Zenaida asiatica* this complex usually arises independently from the subclavian, and in one case it arose from the axillary artery.

Two other branches from the coracoid artery were regularly seen. The first (8) passes across *M. sternocoracoideus* and appears to supply the area of the coracoid articulation with the sternum; the second (7) supplies *M. subcoracoideus* as the main vessel passes between that muscle and the coracoid and penetrates *M. suparacoracoideus.* A small notch on the medial side of the coracoid (shown in Figs. 6 and 7) often marks the passage of the coracoid artery.

All vessels of the coracoid complex are exceedingly variable, in number, size, and site of origin.

A prominent vessel (15) is given off from the posterior pectoral artery, outside the thoracic cavity, passes ventrad, and sends two branches into *M. supracoracoideus.* No corresponding artery was seen in the swallows dissected.

The thoracic artery (3), arising from the pectoral stem, characteristically bifurcates at the anterior end of *M. costi-sternalis.* The dorsal, and larger, branch passes posteriorly, sends several small branches to *M. costi-sternalis,* and continues to the most posterior rib. The ventral trunk bifurcates, one branch passing along the edge of, and supplying, *M. costi-sternalis,* the other

branch passing onto the surface of the sternum. In some specimens two such branches to the sternum were seen.

SUMMARY OF ARTERIAL ARRANGEMENT

In both families the vessels that are relatively constant in appearance are: a subclavian giving rise to the carotid and axillary arteries, and becoming the pectoral trunk; the thoracic artery arising variously, and passing posteriorly to the rib cage; and the coracoid complex of vessels. The coracoid complex includes the coracoid artery, the vessels to *Mm. sternocoracoideus* and *coracobrachialis posterior*, and the sternal artery, which is variously present, and more extensive in some species than in others.

DISCUSSION AND CONCLUSIONS

In the vessels studied individual variation is marked, but the arterial arrangement within both families is relatively constant. Interfamilial differences probably represent responses of the arteries to adaptive structural differences of other systems of the body.

Individual Variation

The term "individual variation" is used here to mean "continuous non-sex-associated variation" (see Mayr, Linsley, and Usinger, 1953:93) found between members of the same species or between the two sides of the same individual. It is hazardous to define individual variation (and also interspecific differences, as discussed later) in the origin of one vessel by relating its location to other vessels, because these may likewise vary in origin. But, by necessity, certain vessels that are probably less variable (axillary, carotid, and pectoral arteries) have been considered here as being constant in origin. If these three vessels are accepted as reference points, individual variants, as well as interspecific differences, can easily be described in the thoracic and coracoid arteries and in their various branches.

The thoracic artery in *P. subis* arose either from the subclavian artery, or from the coracoid artery. Likewise in other swallows, both of these origins were found. In doves the thoracic artery arose consistently from the pectoral stem, lateral to the origin of the axillary artery.

The coracoid artery in *P. subis* and other swallows arose from the subclavian artery, either opposite the base of the axillary artery, or medial to that vessel. In all doves studied the coracoid artery arose from the subclavian medial to the axillary artery. I observed much

individual variation in the branches of the coracoid artery (that is to say, in the vessels of the coracoid complex). In *S. inca* the sternal artery arose either from the coracoid artery, or independently from the subclavian. As mentioned earlier, in members of both families the vessels to *Mm. coracobrachialis posterior* and *subcoracoideus* are highly variable, arising in swallows from the coracoid artery or from the subclavian artery, and in doves from either of these two sites or from the axillary artery. The distribution of these arteries after their origin is also diverse.

Individual variation in the arteries of the thorax has been recorded previously. Bhaduri, Biswas, and Das (1957:2) state that, in the domestic pigeon, "the origin and course of various smaller arteries . . . show noticeable variation," although they do not specifically state to which vessels they are referring. Fisher (1955: 287-288) found variability in the Whooping Crane, *Grus americana*, of the axillary, coracoid, thoracic, and pectoral arteries. In one specimen he found these vessels arising on the right side from the subclavian, in the sequence just listed, and on the left side all arose from the same point. Berger (1956:439-440) strongly emphasized the variability of the vascular system, calling it the most variable in the body. As he stated, this high degree of individual variation seems to be due to the embryological development of the system, wherein many of the adult channels of circulation are derived from embryonic plexuses.

Intrafamilial Differences

In spite of the rather extensive amount of individual variability in some vessels, I found the over-all pattern of arteries to be relatively constant within the family Columbidae and within the family Hirundinidae. There are, nevertheless, several intrafamilial differences needing some further discussion and clarification.

Others have reported the occasional presence of more than one coracoid artery on each side in some columbids, these arteries being described as arising from various sites and being variously named. Bhaduri and Biswas (1954) described the arterial situation in seven species of the family Columbidae (*Columba livia, Streptopelia tranquebarica, S. chinensis, S. senegalensis, Chalcophaps indica, Treron bicincta,* and *T. phoenicoptera*) and stated (*op. cit.*: 348) that "The sterno-clavicular [= coracoid] artery is similar in all the species, but the domestic pigeon seems to be unique in that it has, in addition, a small vessel, the accessory sternoclavicular." This artery was described later, in the domestic pigeon, as

follows (Bhaduri, Biswas, and Das, 1957:5): "A minute and insignificant vessel which has been termed the *accessory sternoclavicular* artery . . . is given off close to the origin of the sternoclavicular. It passes antero-ventrally to supply the adjacent muscles." Glenny (1955:577) described the arterial pattern characteristic of members of the family Columbidae (more than 30 species studied by him) and stated that "three pairs of coracoid arteries are found in *Otidiphaps nobilis,* normally one or two pairs may be found." As suggested by Bhaduri and Biswas (1954:348), the "accessory" vessel probably corresponds to a vessel previously described by Glenny (1940) in *Streptopelia chinensis* and referred to as the "coracoid minor."

Bhaduri and Biswas (1954:348) have suggested that "the accessory sterno-clavicular artery occurring sporadically as it does in some species of diverse groups may not have any phylogenetic value."

In no case did I find more than one coracoid artery on a side. When one of the highly variable arteries feeding *Mm. coracobrachialis posterior* and *sternocoracoideus* (arteries 4 and 4a, Fig. 7) arises from the subclavian or axillary artery instead of from the coracoid artery, that vessel may have been interpreted by others as a second (accessory or minor) coracoid artery. If so, this artery probably does not "occur sporadically." Rather, its origin from the subclavian, axillary, or thoracic artery may be sporadic, subject to individual variation, and it may have been overlooked when it arose from the coracoid artery.

Of the vessels described here, the only one that differed distinctly in one species was the sternal artery. In *Scardafella inca* the right sternal vessel was long, extending down the mid-line of the inner surface of the sternum, whereas in other columbids the right and left arteries ramified on the anterior part of the inner surface of the sternum, or were altogether lacking. I am unable to account for the differential development of this artery in *S. inca.*

In describing the arterial arrangement in the seven species of Indian columbids named earlier, Bhaduri and Biswas (1954:348) state that all species except *Treron phoenicoptera* have two "internal mammary" arteries on each side "showing variable sites of origin." These arteries were later described (Bhaduri, Biswas, and Das, 1957:4-5) as "a slender (*outer*) *internal mammary* artery . . . to the outer wall of the thoracic cavity" and "a slender (*inner*) *internal mammary* artery . . . to supply the inner wall of the chest cavity." From this description, the question arises as to

whether the "outer" one of these arteries should properly be called an *external* instead of *internal* mammary artery. In any case, I saw no specimen possessing two thoracic arteries on a side.

Interfamilial Differences

As shown above, there is a high degree of individual variation in the vessels being considered, while at the same time, few interspecific differences were noted within the families. On the other hand, the vascular arrangement of swallows consistently differed from that of pigeons in the species studied. The differences are most easily described by discussing the resulting change in the site of origin of the thoracic artery. In swallows the thoracic artery arises between the carotid and axillary arteries, either from the stem of the coracoid artery or independently from the subclavian, but in pigeons the thoracic artery arises from the pectoral stem, a site of attachment that is relatively more lateral than in swallows.

This difference, in my opinion, demonstrates well the topological relationships of various systems of the body, here especially of the skeletal, muscular, and vascular systems. The location of the thoracic artery seems to be determined by the particular configuration of skeletal and muscular elements, although even within the bounds set by these elements, individual variation in the precise origin of the artery is possible. In all swallows dissected *Mm. coracobrachialis posterior* and *sternocoracoideus* bridge the angle formed by the costal process and the coracoid. This arrangement makes it necessary for the subclavian to leave the thoracic cavity dorsal to the costal process, although it does pass immediately anterior to that process. The thoracic artery arises from the vessel next to the apex of the costal process, hence from the subclavian, between the axillary and carotid arteries.

In pigeons, the wing of the coracoid extends farther laterally than does the costal process, and the apex of the latter is displaced farther posteriorly than it is in swallows. *M. coracobrachialis posterior* does not arise from the sternum, and only part of the costal process serves as a point of origin for *M. sternocoracoideus.* Consequently, this region differs from that of swallows; the area between the costal process and coracoid is not entirely bridged by muscle, and the space between the two skeletal elements is of a different shape and size. It seems that these differences have resulted, in pigeons, in the subclavian assuming a more anterior position with reference to the costal process. The subclavian in these birds leads into the pectoral artery, which runs posteriad, passing

under *M. sternocoracoideus* and leaving the thoracic cavity approximately opposite the apex of the costal process. The thoracic artery arises immediately opposite the apex of the costal process from the main artery in the area, as it does in swallows, except that in this case the adjacent artery from which it arises is the pectoral stem.

The thoracic area seems to be most "efficiently" arranged when the thoracic artery arises *opposite the apex of the costal process, from whatever main artery is closest to that site.* This arrangement existed in all species studied. Considering the differences in skeletal and muscular structures, between pigeons and swallows, it would be much more remarkable if an alternative were the case, that is to say if the thoracic artery had *the same site of attachment on the subclavian* in both groups.

A comparison of these suggestions with statements made previously about these arteries seems necessary. When Glenny (1955) summarized his accumulative findings, concerning the main arteries in the region of the heart, based on individuals representing more than 750 avian species of 27 orders and 120 families, he described five types of thoracic arteries that were distinguished by differences in the site of their origin, and one type in which there were two thoracic arteries on each side. His statements regarding these differences were as follows (Glenny, 1955:543-544):

"The thoracic, intercostal, or internal mammary artery of birds . . . is found to arise at slightly different relative positions—from a point at the base of the inferior pectoral artery to a point near the base of the coracoid or sternoclavicular artery, and in some instances both of these vessels have a common root from the subclavian artery. Such differences are found to be of common occurrence within several orders of birds. In the Galliformes and the Passeriformes there appears to be a graded series in the sites of attachment of the thoracic artery from a lateral to a medial position. As a result of these observations, numerical values can be assigned to the site of attachment of the intercostal or thoracic artery, and these values may come to be used as an index in specific levels of evolution. . . .

"The medial migration of the thoracic artery appears to have some phylogenetic significance as yet not understood."

The six types of thoracic arteries described in Glenny's classification were distinguished as follows (Glenny, 1955:544):

"Type 1: attachment to the pectoral stem lateral to the axillary.

"Type 2: attachment to the subclavian between the axillary and coracoid.

"Type 3: attachment to the subclavian at the base of the coracoid.

"Type 4: attachment to the subclavian, but with a common root for both the coracoid and thoracic.

"Type 5: attachment to the subclavian medial to both the axillary and coracoid.

"Type 6: two separate thoracic arteries are present; the primary thoracic is the same as type 1 above, while the secondary thoracic is the same as type 3 or type 4 above."

Possibly the thoracic artery has undergone migration but apparent differences in its origin might well be due to differences in other vessels of the thoracic area. Additionally, there seems to be no reason to assume that the lateral position of the thoracic artery is the primitive one, or that the medial is the derived position, as is implied by the phrase "medial migration." Although the lateral site of attachment (type 1) is predominant in the lower orders of birds, and the medial attachment is found primarily in Passeriformes, a fact which may indicate that type 1 is the more primitive, it must nevertheless be kept in mind that a sequence of a single morphological character does not necessarily represent the phylogenetic sequence of the character itself (see Mayr, 1955:41).

Also, a given arterial arrangement might be independently derived more than once. If such has been the case, similarities in arterial arrangements in different taxa would sometimes be "chance similarities," that is to say, "resemblance in characteristics developed in separate taxa by independent causes and without causal relationship involving the similarity as such" (Simpson, 1961:79).

The particular arrangement of the arteries of the thoracic area also seems to be of limited value as a clue to taxonomic relationships. If the origin of any artery is determined by skeletal and muscular features, as I suggest, the artery perhaps ought not be considered as a separate character, but as part of a "character complex" that varies as a unit (see Mayr, Linsley, and Usinger, 1953: 123). The skeleton offers a potential fossil record for consideration. Changes in the skeleton and muscles, great enough to affect the blood vessels, would probably be detected more easily than would the resulting vascular changes. Also, I did not find as much individual variation in the skeleton and muscles in the area studied as I did in the vascular system. In other words, within the bounds established by the skeletal and muscular features, the artery still exhibited individual variation in exact origin.

SUMMARY

The origin, distribution, and individual variation of the thoracic and coracoid arteries, and their branches, have been studied in four species of the family Columbidae (pigeons) and in five species of the family Hirundinidae (swallows). These arteries are described for *Scardafella inca* (Inca Dove) and *Progne subis* (Purple Martin). Muscles that are supplied by these vessels, and muscles the partic-

ular configuration of which seems to effect the arrangement of the arteries have also been described. Correlation of the arteries observed with those named and described by other workers has been attempted.

In most of the vessels studied there is a high degree of individual variation, but few interspecific differences were noticed within either family. Differences in the arteries of the thorax between the two families are described by discussing the resulting different origins of the thoracic artery. In swallows the thoracic artery arises from either the subclavian artery or the coracoid artery, whereas in pigeons it arises from the pectoral trunk. This difference in site of attachment seems to be a result of differences between the two families in muscular and skeletal elements of the thorax.

The particular site of attachment of the thoracic artery is of limited value as a taxonomic character. Several considerations influenced this conclusion. (1) If the location of the artery is determined by skeletal and muscular elements, these associated structures must be considered taxonomically as a "character complex" (a set of characters varying as a unit). (2) Even within the bounds established by the skeleton and muscles, the artery displays a high degree of individual variation in exact origin. (3) A given arterial arrangement could have been derived independently many times. (4) Because differences are defined relative to other likewise variable vessels, supposed similarities or differences in the one artery may be artifacts of the system of description.

My findings and interpretations do not support previous suggestions that the thoracic artery has undergone a mediad migration, and that the various sites of attachment of that vessel may come to represent various levels of evolution. The primitive site of attachment of the vessel is unknown, and it seems to me that it has not been sufficiently demonstrated that the vessel has undergone any "migration."

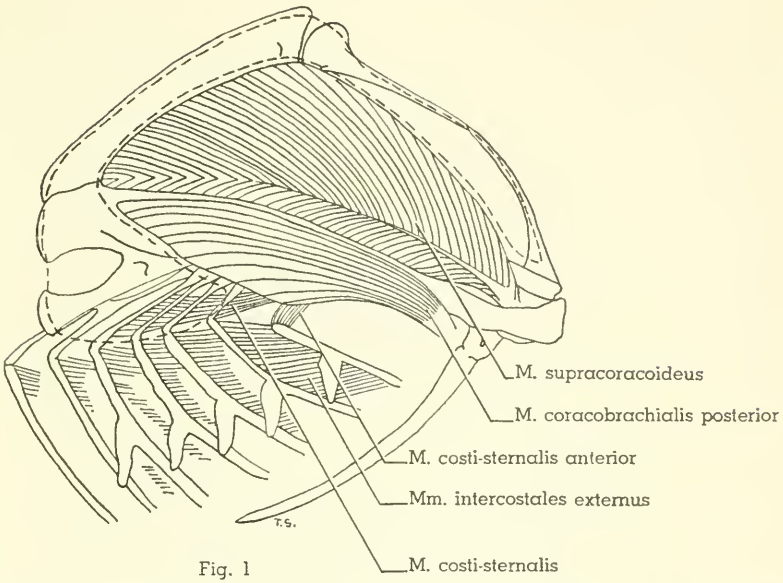


Fig. 1

FIG. 1. *Progne subis.* Lateral view of left half of thorax. *M. pectoralis thoracica* (area of insertion indicated by dotted line) has been removed. Muscles not described in text are not shown. (× 1.5.)

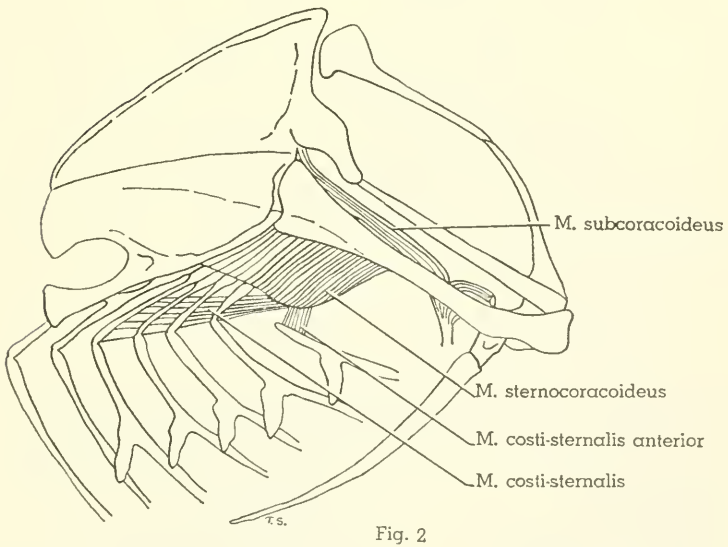
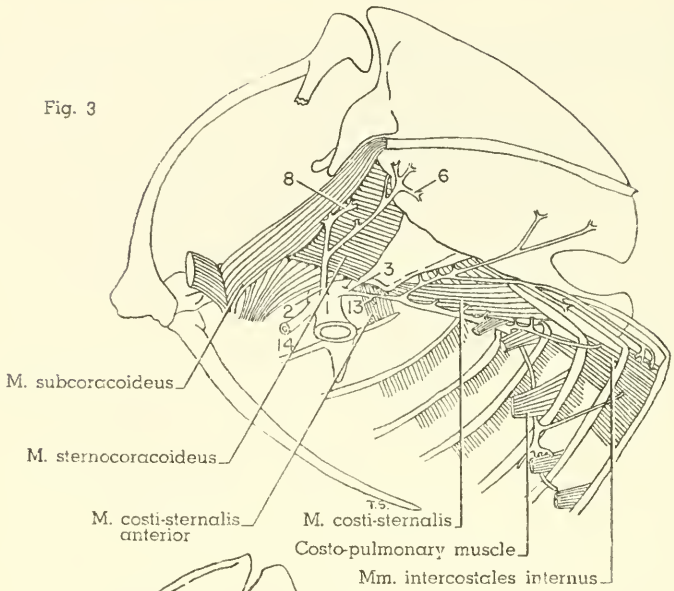


Fig. 2

FIG. 2. *Progne subis.* Lateral view of left half of thorax. Same view as shown in Fig. 1, but with *Mm. supracoracoideus, coracobrachialis posterior,* and *intercostales externus* removed. (× 1.5.)



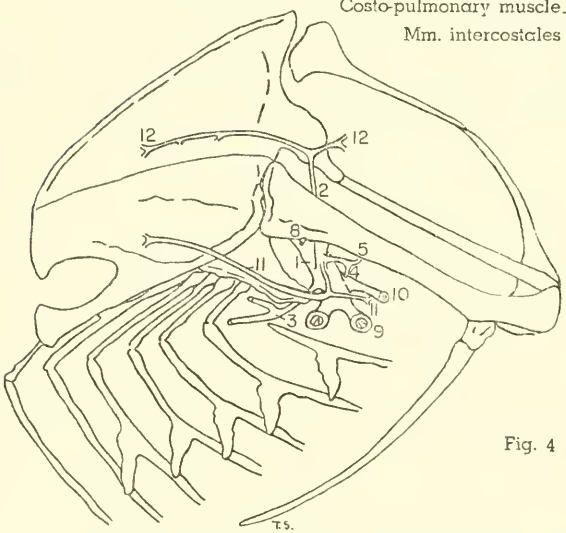


FIG. 3. *Progne subis.* Medial view of left half of thorax. Not all muscles shown. See Fig. 4 for identification of arteries. (× 1.5.)

FIG. 4. *Progne subis.* Lateral view of left half of thorax. (× 1.5.)

(Applies also to Fig. 3.)

1. Subclavian artery.
2. Coracoid artery.
3. Thoracic artery.
4. (Unnamed.) Supplies *M. coracobrachialis posterior.*
5. (Unnamed.) Supplies *M. subcoracoideus.*
6. (Unnamed.) Supplies *M. sternocoracoideus* and sternum.
7. (Unnamed.) Supplies *M. subcoracoideus.*
8. (Unnamed.) Supplies *M. sternocoracoideus, M. coracobrachialis posterior,* and sternum.
9. Pectoral artery.
10. Axilliary artery.
11. (Unnamed.) Supplies *M. coracobrachialis posterior.*
12. (Unnamed.) Supplies *M. supracoracoideus.*
13. (Unnamed.) Supplies *M. costi-sternalis anterior.*
14. Carotid artery.

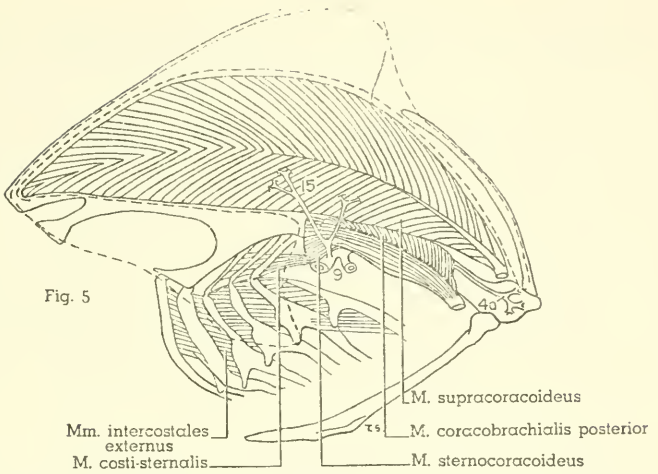


FIG. 5. *Scardafella inca.* Lateral view of left half of thorax. *M. pectoralis thoracica* (area of insertion indicated by dotted line) has been removed. Muscles not described in text are not shown. See legend for Fig. 7 for identification of arteries. (× 1.)

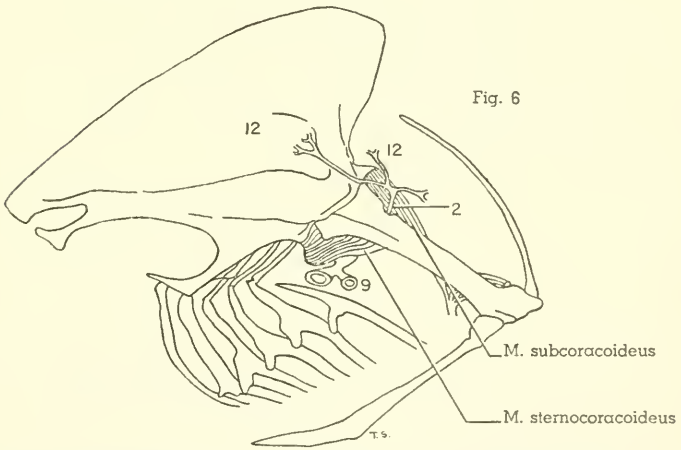


FIG. 6. *Scardafella inca.* Lateral view of left half of thorax. See legend for Fig. 7 for identification of arteries. (× 1.)

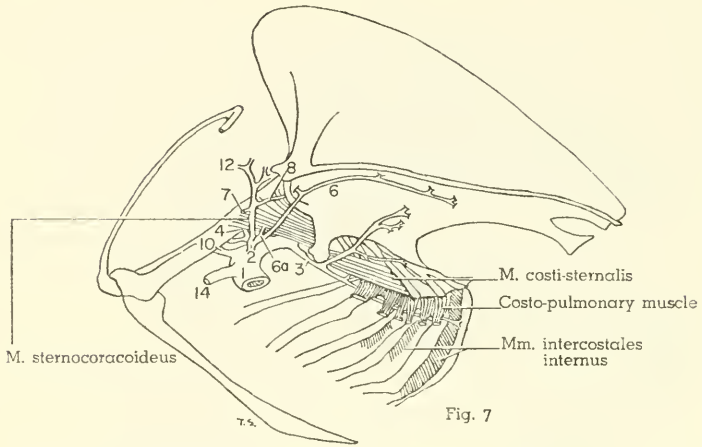


FIG. 7. *Scardafella inca.* Medial view of left half of thorax. (× 1.)

KEY

(Applies also to Figs. 5 and 6.) Numerals not used are those used for *Progne subis* for which no homologous artery occurs in *Scardafella inca.*

1. Subclavian artery.
2. Coracoid artery.
3. Thoracic artery.
4. (Unnamed.) Supplies *Mm. coracobrachialis posterior* and *sternocoracoideus.*
4a. (Unnamed.) Supplies *M. coracobrachialis posterior.*
6. Sternal artery. (Shown as it appears on *right* side. Left sternal artery not so extensive.)
6a. (Unnamed.) Supplies *M. sternocoracoideus.*
7. (Unnamed.) Supplies *M. subcoracoideus.*
8. (Unnamed.) Supplies coracoid-sternal articulation.
9. Pectoral artery.
10. Axillary artery.
12. (Unnamed.) Supplies *M. supracoracoideus.*
14. Carotid artery.
15. (Unnamed.) Supplies *M. supracoracoideus.*

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The Breeding Birds of Kansas

BY

RICHARD F. JOHNSTON

UNIVERSITY OF KANSAS
LAWRENCE
1964

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21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.

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INTRODUCTION

The breeding avifauna of Kansas has received intermittent attention from zoologists for about 75 years. Summary statements, usually concerning all birds of the state, have been published by Goss (1891), Long (1940), Goodrich (1941), Tordoff (1956) and Johnston (1960). All but the first dealt with the breeding birds chiefly in passing, and none was concerned primarily with habitat distributions and temporal characteristics of Kansan birds. The present work treats mainly certain temporal relationships of breeding birds in Kansas, but also geographic distribution, habitat preferences, and zoogeographic relationships to the extent necessary for a useful discussion of temporal breeding phenomena.

Information on breeding of some of the 176 species of birds known to breed in Kansas is relatively good, on a few is almost nonexistent, and on most is variously incomplete. It is nevertheless possible to make meaningful statements about many aspects of the breeding biology and distribution of most species of Kansan birds;

we can take stock, as it were, of available information and assess the outstanding avenues of profitable future work. In the accounts of species below, the information given is for the species as it occurs in Kansas, unless it is otherwise stated. For the various subsections analyzing biology and distribution, only information taken in Kansas is used, and for this reason the analyses are made on about half the species breeding in the state. An enormous amount of observational effort has been expended by several dozen people in order that suitable data about breeding birds of Kansas be available; all persons who have contributed in any way are listed in the section on acknowledgments, following the accounts of species.

Kansas has been described topographically, climatically, and otherwise ecologically many times in the recent past; the reader is referred to the excellent account by Cockrum (1952), which treats these matters from the viewpoint of a zoologist. For present purposes it will suffice to mention the following characteristics of Kansas as a place lived in by birds.

Topographically, Kansas is an inclined plane having an elevation of about 4100 feet in the northwest and about 700 feet in the southeast. West of approximately 97° W longitude, the topography is gently rolling, low hills or flat plain; to the east the Flint Hills extend in a nearly north to south direction, and to the east of these heavily weathered, grassy hills is a lower-lying but more heavily dissected country, hills of which show no great differences in elevation from surrounding flatland.

The vegetation of eastern Kansas comingles with that of the western edge of the North American deciduous forest; a mosaic of true forest, woodland remnants, and tall-grass prairie occupies this area east of the Flint Hills. From these hills west the prairie grassland today has riparian woodland along watercourses; the prairie is composed of proportionally more and more short-grass elements to the west and tall-grass elements to the east.

Climate has a dominating influence on the vegetational elements sketched above. Mean annual rainfall is 20 inches or less in western sectors and increases to about 40 inches in the extreme eastern border areas. Mean monthly temperatures run from 25°F. or 30°F. in winter to 80°F. or 90°F. in summer. The northwestern edges of Caribbean Gulf warm air masses regularly reach northward only to the vicinity of Doniphan County, in northeastern Kansas, and extend southwestward into west-central Oklahoma; these wet frontal systems are usually dissipated along the line indicated by masses of

arctic air, sometimes in spectacular fashion. The regular recurrence of warm gulf air is responsible for the characteristically high relative humidity in summer over eastern Kansas and it has an ameliorating effect on winter climate in this region. Almost immediately to the north in Nebraska and to the west in the high plains, summers are dryer and winters are notably more severe. The breeding distributions of some species of birds fairly closely approximate the distribution of these warm air masses; these examples are noted where appropriate below.

DISTRIBUTION OF BIRDS IN KANSAS

Birds breeding in Kansas are taxonomically, ecologically, and distributionally diverse. Such diversity is to be expected, in view of the midcontinental position of the State. Characteristics of insularity, owing to barriers to dispersal and movement, tend to be lacking in the makeup of the avifauna here. The State is not, of course, uniformly inhabited by all 176 species (Table 1) of breeding birds; most species vary in numbers from one place to another, and some are restricted to a fraction of the State. Variations in numbers and in absolute occurrence are chiefly a reflection of restriction or absence of certain plant formations, which is to say habitats; the analysis to follow is thus organized mainly around an examination of gross habitat-types and the birds found in them in Kansas.

TABLE 1.—THE BREEDING BIRDS OF KANSAS

Woodland Species

Elanoides forficatus N*
Ictinia misisippiensis U
Accipiter striatus U
A. cooperii U
Buteo jamaicensis O
B. lineatus N
B. platypterus N
Aquila chrysaëtos O
Falco sparverius U
Colinus virginianus N
Phasianus colchicus O
Meleagris gallopavo N
Philohela minor U
Zenaidura macroura N
Ectopistes migratorius N
Conuropsis carolinensis U
Coccyzus americanus N
C. erythropthalmus N
Otus asio U
Bubo virginianus O
Strix varia U
Asio otus U
Aegolius acadicus U
Caprimulgus carolinensis N
C. vociferus U
Phalaenoptilus nuttallii N
Chaetura pelagica U
Archilochus colubris N
Colaptes auratus N
C. cafer N
Dryocopus pileatus O
Centurus carolinus N
Melanerpes erythrocephalus N
Dendrocopos villosus O
D. pubescens O
Tyrannus tyrannus S
T. vociferans S
Muscivora forficata S
Myiarchus crinitus S
Sayornis phoebe S
Empidonax virescens S
Contopus virens S
Iridoprocne bicolor N
Progne subis N
Cyanocitta cristata N
Pica pica O

Corvus brachyrhynchos O
C. cryptoleucus O
Parus atricapillus O
P. carolinensis O
P. bicolor O
Sitta carolinensis O
Troglodytes aedon N
Thryomanes bewickii N
Thryothorus ludovicianus N
Mimus polyglottos N
Dumetella carolinensis N
Toxostoma rufum N
Turdus migratorius O
Hylocichla mustelina N
Sialia sialis O
Bombycilla cedrorum N
Lanius ludovicianus O
Sturnus vulgaris O
Vireo atricapillus N
V. griseus N
V. bellii N
V. flavifrons N
V. olivaceus N
V. gilvus N
Mniotilta varia N
Protonotaria citrea N
Parula americana N
Dendroica aestiva N
D. discolor N
Seiurus motacilla N
Oporornis formosus N
Icteria virens N
Wilsonia citrina N
Setophaga ruticilla N
Passer domesticus O
Icterus spurius N
I. galbula N
I. bullockii N
Quiscalus quiscula N
Molothrus ater N
Piranga olivacea N
P. rubra N
Richmondena cardinalis S
Pheucticus melanocephala S
P. ludoviciana S
Guiraca caerulea S
Passerina ciris S
P. cyanea S
P. amoena S
Spinus pinus O
S. tristis O
Loxia curvirostra O
Pipilo erythrophthalmus N
Chondestes grammacus N
Spizella passerina N

Limnic Species

Podilymbus podiceps U
Phalacrocorax auritus U
Ardea herodias U
Leucophoyx thula U
Nycticorax nycticorax U
Nyctanassa violacea U
Ixobrychus exilis U
Botaurus lentiginosus U
Plegadis chihi U
Branta canadensis U
Anas platyrhynchos U
A. acuta U
A. discors U
A. clypeata U
Aix sponsa U
Aythya americana U
Oxyura jamaicensis U
Rallus elegans U
Butorides virescens U
Florida caerulea U
Casmerodius albus U
Porzana carolina U
Laterallus jamaicensis U
Gallinula chloropus U
Fulica americana U
Charadrius alexandrinus U
Actitis macularia U
Steganopus tricolor U
Sterna albifrons U
Chlidonias niger U
Telmatodytes palustris N
Cistothorus platensis N
Geothlypis trichas N
Xanthocephalus xanthocephalus N
Agelaius phoeniceus N
Rallus limicola U

Grassland Species

Buteo swainsonii N
B. regalis U
Circus cyaneus O
Tympanuchus cupido N
T. pallidicinctus N
Pedioecetes phasianellus N
Charadrius vociferus U
Eupoda montana U
Numenius americanus U
Bartramia longicauda U
Speotyto cunicularia U
Asio flammeus U
Sayornis saya S
Eremophila alpestris O
Dolichonyx oryzivorus N
Sturnella magna N
S. neglecta N
Spiza americana N
Calamospiza melanocorys N
Ammodramus savannarum N
Passerherbulus henslowii N
Aimophila cassinii N
Spizella pusilla N

Xeric Scrub Species

Callipepla squamata N — *Geococcyx californianus* N
Salpinctes obsoletus N

Unanalyzed Species

Cathartes aura N — *Chordeiles minor* U
Coragyps atratus N — *Megaceryle alcyon* U
Falco peregrinus U — *Riparia riparia* O
Columba livia O — *Stelgidopteryx ruficollis* N
Tyto alba U — *Hirundo rustica* O
Petrochelidon pyrrhonota U

[a] The letter following each name refers to presumed zoogeographic derivation of the species, modified after Mayr (1946). N = North American evolutionary stock; S = South American stock; O = Eurasian stock; U = unanalyzed.

Avian Habitats in Kansas

Four major habitat-types can be seen in looking at the distribution of the breeding avifauna of Kansas. These are woodland, grassland, limnic, and xeric scrub plant formations. A little more than half the breeding birds of Kansas live in woodland habitats, about one-fifth in limnic habitats, about one-eighth in grassland habitats, and less than two per cent in scrub habitats; this leaves some 6.4 per cent of the breeding avifauna unanalyzed (Table 2).

Woodland Habitats

One hundred one species of Kansan birds are woodland species (tables 1 and 2). The analysis of Udvardy (1958) showed woodland birds to be the largest single avifaunal element in North America, with 38 per cent of North American birds relegated to it. It is likewise the largest element in the Kansan avifauna, representing 58 per cent of Kansan birds. Although woodland makes up

TABLE 2.—ANALYSIS OF THE BREEDING AVIFAUNA OF KANSAS BY HABITAT-TYPES

HABITAT-TYPE	Percentage of the Avifauna of		
	Kansas	North America	Stated habitat
Woodland: 101 species	58	16.7	44.4
Limnic: 36 species [1]	21	6.0	38.5
Grassland: 23 species	13	3.8	71.3
Xeric scrub: 3 species	2	0.5	10.2
Unanalyzed: 11 species	6	2.0	55.0
Totals: 174 species	100	29.0	43.2

1. Does not include the Canvasback (*Aythya valisineria*), the Forster Tern (*Sterna forsteri*), and the Black Tern (*Chlidonias niger*), all recently added to the breeding avifauna of Kansas.

a relatively small fraction of the vegetational complexes in Kansas, a large number of habitats exist in what woodland is present. An even larger number of possible woodland habitats is clearly missing, however, because the 101 Kansan species actually represent but 44 per cent of all woodland birds in North America, according to Udvardy's analysis. Broad-leaved, deciduous woodlands in Kansas are of restricted horizontal and vertical stratification. More complex deciduous forest associations and all coniferous forest associations are absent from the State.

Using Mayr's (1946) breakdown of geographical origin of the North American bird fauna, about 53 per cent of the woodland passerine birds in Kansas are of "North American" origin, 22 per cent are of "Eurasian" origin, and 14 per cent are of "South American" origin (Table 3). These figures for Kansas are commensurate with those found for other geographic districts at the same latitude

TABLE 3.—ANALYSIS OF ECOLOGIC GROUPS OF BIRDS BY STATUS OF RESIDENCY AND AREA OF ORIGIN

	Migrant	Resident	Pt. Migr.	Old World	N. Amer.	S. Amer.	Unanalyzed
Woodland species 101:58%	60%	29%	11%	22%	53%	14%	11%
Limnic species 36:21%	94%	0	6%	0	14%	0	86%
Grassland species 23:13%	61%	26%	13%	9%	56%	3%	30%
Xeric Scrub species 3:2%	33%	66%	0	0	100%	0	0
Unanalyzed species 11:6%	64%	27%	9%	26%	26%	0	48%

in North America (Mayr, 1946:28). Other characteristics of woodland birds are summarized in tables 4 and 5.

Limnic Habitats

Of Kansan birds, 36 species (20 per cent) prefer limnic habitats (Table 1). Udvardy found this group to represent 15 per cent of the North American avifauna. Kansas is not notably satisfactory for limnic species, and only 38 per cent of the total North American limnic avifauna is present in the State.

Thirty-one species of limnic birds belong to families that Mayr (1946) considered to be unanalyzable as to their geographic origin; of the five remaining species, all seem to be of North American

origin. Other characteristics of limnic birds are summarized in tables 4 and 5.

Grassland Habitats

Twenty-three species of our total can be called grassland species (Table 1). The subtotal is less than one-fifth of the Kansan avi-

TABLE 4.—ANALYSIS BY HABITAT-TYPE AND RESIDENCY STATUS OF HISTORIC AVIAN STOCKS IN KANSAS

	Woodland	Limnic	Grassland	Xeric Scrub	Unanal. Hab.	Migrant	Resident	Partly Migrant
Old World Element.. 27:16%	80%	0	8%	0	12%	11%	78%	11%
North American Element..... 77:44%	69%	6%	17%	4%	4%	72%	14%	14%
South American Element..... 15:8%	93%	0	7%	0	0	93%	7%	0
Unanalyzed Origin.. 53:32%	22%	56%	13%	0	9%	79%	16%	5%

fauna, but it represents 72 per cent of the grassland birds of North America; grassland habitats abound in Kansas. Only 5.3 per cent of all North American birds are grassland species (Udvardy, 1958).

About 56 per cent of these birds are of North American stocks, nine per cent of Eurasian stocks, and three per cent of South American stocks. The percentage of North American species is the greatest for any habitat group here considered. Other characteristics of grassland birds are summarized in tables 4 and 5.

Xeric-Scrub Habitats

Three species of Kansan birds can be placed in this category (Table 1). This is less than one per cent of the North American avifauna, two per cent of the Kansan avifauna, and ten per cent of the birds of xeric scrub habitats in North America. The three species are considered to be of North American origin.

Unanalyzed as to Habitat

Eleven species of Kansan birds could not be assigned to any of the habitat-types mentioned above. The total represents two per

TABLE 5.—ANALYSIS BY ECOLOGIC STATUS AND AREA OF ORIGIN OF MIGRANT AND RESIDENT BIRDS

	Woodland	Limnic	Grassland	Xeric Scrub	Unanal. Hab.	Old World	North America	South America	Unanalyzed
Migrant species... 117:67%	52%	29%	12%	1%	6%	2%	49%	12%	37%
Resident species... 40:23%	73%	0	15%	5%	7%	51%	26%	2%	21%
Partly migrant.. 17:10%	64%	11%	17%	0	6%	17%	66%	0	17%

cent of the North American avifauna, six per cent of the birds of Kansas, and 55 per cent of the species reckoned by Udvardy (*loc. cit.*) to be unanalyzable. Fifty-five per cent is a large fraction, but only to be expected: species are considered unanalyzable if they show a broad, indiscriminate use of more than one habitat-type, and such birds tend to be widely distributed.

Species Reaching Distributional Limits in Kansas

The distributional limits of a species are useful in indicating certain of its adaptive capacities and implying maintenance of or shifts in characteristics of habitats. Although it is generally an oversimplification to ignore abundance when treating of distribution, the present remarks of necessity do not pertain to abundance.

Western Limits Reached in Kansas

Thirty-one species (tables 6 and 7) reach the western limits of their distribution somewhere in Kansas. Most of these limits are in eastern Kansas, and coincide with the gradual disappearance of

TABLE 6.—BREEDING BIRDS REACHING DISTRIBUTIONAL LIMITS IN KANSAS

Species reaching northern distributional limits

Florida caerulea
Leucophoyx thula
Coragyps atratus
Elanoides forficatus
Ictinia misisippiensis
Tympanuchus pallidicinctus
Callipepla squamata
Geococcyx californianus
Caprimulgus carolinensis
Muscivora forficata
Parus carolinensis
Vireo atricapillus
Passerina ciris
Aimophila cassinii

Species reaching southern distributional limits

Aythya americana
Parus atricapillus
Bombycilla cedrorum
Dolichonyx oryzivorus
Pedioecetes phasianellus
Empidonax minimus
Steganopus tricolor
Chlidonias niger
Coccyzus erythropthalmus

Species reaching eastern distributional limits

Eupoda montana
Numenius americanus
Phalaenoptilus nuttallii
Colaptes cafer
Tyrannus verticalis
Sayornis saya
Corvus cryptoleucus
Salpinctes obsoletus
Icterus bullockii
Pheucticus melanocephalus
Passerina amoena

Species reaching western distributional limits

Aix sponsa
Buteo platypterus
Philohela minor
Ectopistes migratorius
Conuropsis carolinensis
Chaetura pelagica
Archilochus colubris
Dryocopus pileatus
Centurus carolinus
Myiarchis crinitus
Empidonax virescens
E. traillii
Parus bicolor
Thryothorus ludovicianus
Cistothorus platensis
Hylocichla mustelina
Vireo griseus
V. flavifrons
Mniotilta varia
Protonotaria citrea
Parula americana
Dendroica discolor
Seiurus motacilla
Oporornis formosus
Wilsonia citrina
Setophaga ruticilla
Sturnella magna
Piranga olivacea
Pheucticus ludovicianus
Pipilo erythrophthalmus
Passerherbulus henslowii

the eastern deciduous forest formation. Twenty-nine species are woodland birds, and few of these seem to find satisfactory conditions in the riparian woods extending out through western Kansas. The Wood Thrush is the one woodland species that has been found nesting in the west (Decatur County; Wolfe, 1961). Descriptively, therefore, the dominant reason for the existence of distributional limits in at least 28 of these birds is the lack of suitable woodland in western Kansas; these 28 are the largest single group reaching distributional limits in the State. Many other eastern woodland birds occur in western Kansas along riparian woodlands, as is mentioned below.

Two species showing western limits in Kansas are characteristic of grassland habitats; the Eastern Meadowlark seems to disappear with absence of moist or bottomland prairie grassland and the Henslow Sparrow may be limited westerly by disappearance of tall-grass prairie.

The Short-billed Marsh Wren, a marginal limnic species, reaches its southwesterly mid-continental breeding limits in northeastern

Kansas. The species breeds in Kansas in two or three years of each ten, in summers having unusually high humidity.

Northern Limits Reached in Kansas

Fourteen species (tables 6 and 7) reach their northern distributional limits in Kansas. Eight of these are birds of woodland habitats, but of these only the Carolina Chickadee is a species of the eastern deciduous woodlands; the other seven live in less mesic woodland. Three of these species (Chuck-will's-Widow, Scissor-tailed Flycatcher and Painted Bunting) have breeding ranges that suggest the northwesterly occurrences of summer humid warm air masses ("gulf fronts") and this environmental feature perhaps is of major importance for these birds, as it is also for the vegetational substratum in which the birds live.

The Lesser Prairie Chicken and the Cassin Sparrow are the two birds of grasslands that are limited northerly in Kansas. Xeric, sandy grassland is chiefly limited to the southwestern quarter of Kansas, and this limitation is perhaps of major significance to these

TABLE 7.—ANALYSIS BY HABITAT-TYPE OF BIRDS REACHING DISTRIBUTIONAL LIMITS IN KANSAS

DIRECTIONAL LIMIT	Habitat-types				
	Woodland	Grassland	Limnic	Xeric Scrub	Total
Western extent.....	28	2	1	0	31
Northern extent....	8	2	2	2	14
Eastern extent.....	6	4	0	1	11
Southern extent....	4	2	3	0	9
Totals.....	46	10	6	3	65
Per cent of the Species in Stated Habitat.....	46	43	14	100	37

two species. The Scaled Quail and Roadrunner tend to drop out as the xeric "desert scrub" conditions of the southwest drop out in Kansas.

Eastern Limits Reached in Kansas

Eleven species (tables 6 and 7) reach their eastern distributional limits in Kansas. Six of these are woodland birds. Four of these are members of well-known species-pairs: the Red-shafted Flicker, Bullock Oriole, Black-headed Grosbeak, and Lazuli Bunting. Presence to the east of complementary species has much to do with the

absence of these species in eastern Kansas. Four of the eleven are birds of grasslands, and they drop out as the short-grass prairie is restricted easterly.

The Rock Wren may be considered characteristic of xeric scrub in Kansas, and it is not found to the east in the absence of such scrub.

Southern Limits Reached in Kansas

Eight species (tables 6 and 7) reach their southern distributional limits in Kansas. Half of these birds are of woodland habitats, and of these four, the Black-capped Chickadee and Cedar Waxwing are chiefly of sub-boreal distribution. The Black-capped Chickadee also finds its niche partly pre-empted in southern Kansas by the Carolina Chickadee.

The Bobolink and Sharp-tailed Grouse are grassland species that are seemingly adapted to cooler, dryer grassland than is found in most of Kansas.

The Redhead, Wilson Phalarope, and Black Tern are limnic species, perhaps limited southerly by high summer temperatures; the three species are entirely marginal anywhere in Kansas.

Influence of Riparian Woodland

Although the largest single element of the Kansan avifauna that reaches distributional limits in Kansas is made up of birds of the eastern deciduous forest, several species of the eastern woodlands are present in Kansas along the east-west river drainages in riparian woodland; the species are listed in Table 8. Twenty-one kinds are involved if we include the Cooper Hawk, Yellow-billed Cuckoo, Orchard Oriole, Summer Tanager, Rufous-sided Towhee, and Chipping Sparrow, all of which breed farther to the west but are present in western Kansas only along river drainages. This leaves 15 species of eastern deciduous woodlands that occur west in Kansas along

TABLE 8.—BIRDS OF THE EASTERN DECIDUOUS FOREST FOUND IN WESTERN KANSAS IN RIPARIAN WOODLAND

Accipiter cooperii °
Coccyzus americanus °
Centurus carolinus
Melanerpes erythrocephalus
Tyrannus tyrannus
Myiarchus crinitus
Contopus virens
Sayornis phoebe
Cyanocitta cristata
Dumetella carolinensis
Toxostoma rufum
Sialia sialis
Vireo olivaceus
Icterus spurius °
Icterus galbula
Quiscula quiscalus
Piranga rubra °
Passerina cyanea
Richmondena cardinalis
Pipilo erythrophthalmus °
Spizella passerina °

° Breeds farther west in North America in other types of vegetation.

riparian woodland (*versus* 30 species that drop out chiefly where eastern woodland drops out). These 15 species are about one-third of all woodland birds in western Kansas. Riparian woodland does not seem to afford first-rate habitat for most of the eastern woodland species that do occur; breeding density seems to be much lower than in well-situated eastern woodland.

The importance of these linear woodlands as avenues for gene-flow between eastern and western populations, especially of species-pairs (grosbeaks, flickers, orioles, and buntings), is obviously great. Likewise significant is the existence of these alleys for dispersal from the west of certain species (for instance, the Black-billed Magpie and the Scrub Jay) into new but potentially suitable areas.

BREEDING SEASONS

Introduction

An examination of breeding seasons or schedules is properly undertaken at several levels. The fundamental description of variation in breeding schedules must itself be detailed in several ways and beyond this there are causal factors needing examination. The material below is a summary of the information on breeding schedules of birds in Kansas, treated descriptively and analytically in ways now thought to be of use.

Almost any event in actual reproductive activity has been used in the following report; nestbuilding, egg-laying, incubation, brooding of young, feeding of young out of the nest are considered to be of equal status. To any such event days are added or subtracted from the date of observation so as to yield the date when the clutch under consideration was completed.

Such corrected dates can be used in making histograms that show the time of primary breeding activity, or the "egg-season." All such schedules are generalizations; data are used for a species from any year of observation, whether 50 years ago or less than one year ago. One advantage of such procedure is that averages and modes are thus more nearly representative of the basic temporal adaptations of the species involved, as is explained below.

When information on the schedule of a species from one year is lumped with information from another year or other years, two (and ordinarily more than two) frequency distributions are used to make one frequency distribution. The great advantage here is that the frequency distribution composed of two or more frequency distributions is more stable than any one of its components. Second, the peak of the season, the mode of egg-laying, is represented more

broadly than it would have been for any one year alone. Third, the extremes of breeding activity are fairly shown as of minute frequency and thus of limited importance, which would not be true if just one year were graphed. All these considerations combine to support the idea that general schedules in fact represent the basic temporal adaptations of a species much better than schedules for one year only.

Variation in Breeding Seasons

In the chronology of breeding seasons of birds, there are three basic variables: time at which seasons begin, time at which seasons end, and time in which the major breeding effort occurs. These variables have been examined in one population through time (Lack, 1947; Snow, 1955; Johnston, 1956) in several populations of many species over wide geographic ranges (Baker, 1938; Moreau, 1950; Davis, 1953), and in several populations of one species (Lack, *loc. cit.;* Paynter, 1954; Johnston, 1954). The analysis below is concerned with breeding of many kinds of birds of an arbitrarily defined area and with the influence of certain ecologic and zoogeographic factors on the breeding seasons for those several species.

THE INFLUENCE OF SEASONAL STATUS.—Here we are interested in whether a species is broadly resident or migrant in Kansas; 70 species are available for analysis.

Resident Species

Twenty-four species, furnishing 875 records of breeding, are here considered to be resident birds in northeastern Kansas. These species are Cooper Hawk, Red-tailed Hawk, Prairie Chicken, Bobwhite, Rock Dove, Great Horned Owl, Red-bellied Woodpecker, Hairy Woodpecker, Downy Woodpecker, Horned Lark, Blue Jay, Common Crow, Black-billed Magpie, Black-capped Chickadee, Tufted Titmouse, Carolina Wren, Bewick Wren, Mockingbird, Eastern Bluebird, Loggerhead Shrike, Starling, House Sparrow, Eastern Meadowlark, and Cardinal. The distribution of completed clutches (Fig. 1) runs from mid-January to mid-September, with a modal period in the first third of May. Conspicuous breeding activity occurs from mid-April to the first third of June.

Migrant Species

Forty-six species, furnishing 2,522 records of breeding, are considered to be migrant in northeastern Kansas. These species are Great Blue Heron, Green Heron, Swainson Hawk, American Coot,

Killdeer, Upland Plover, American Avocet, Least Tern, Yellow-billed Cuckoo, Black-billed Cuckoo, Burrowing Owl, Common Nighthawk, Chimney Swift, Red-headed Woodpecker, Eastern Kingbird, Western Kingbird, Scissor-tailed Flycatcher, Great Crested Flycatcher, Eastern Phoebe, Eastern Wood Pewee, Bank Swallow, Rough-winged Swallow, Barn Swallow, Purple Martin, Brown Thrasher, Catbird, House Wren, Robin, Wood Thrush, Blue-gray Gnatcatcher, Bell Vireo, Warbling Vireo, Prothonotary Warbler, Yellow Warbler, Chat, Western Meadowlark, Red-winged Blackbird, Orchard Oriole, Baltimore Oriole, Common Grackle, Black-headed Grosbeak, Indigo Bunting, Dickcissel, Lark Sparrow, and Field Sparrow. The distribution of completed clutches runs from mid-March to the first third of September, with a modal period of egg-laying in the first third of June (Fig. 1). Conspicuous breeding activity occurs from the first third of May to the last third of June.

THE INFLUENCE OF DOMINANT FORAGING ADAPTATION.—Five categories here considered reflect broad foraging adaptation: woodland species, taking invertebrate foods in the breeding season from woody vegetation or the soil within wooded habitats; grassland species, taking invertebrate foods in the breeding season from within grassland situations; limnic species, foraging within marshy or aquatic habitats; aerial species, foraging on aerial arthropods; raptors, feeding on vertebrates or large insects.

Raptors

Six species, furnishing 174 records of breeding, are here considered, as follows: Cooper Hawk, Red-tailed Hawk, Swainson Hawk, Great Horned Owl, Burrowing Owl, and Loggerhead Shrike. The distribution of clutches (Fig. 1) runs from mid-January to the first third of July and is bimodal. One period of egg-laying occurs in mid-February and a second in the last third of April. Such a distribution indicates that two basically independent groups of birds are being considered. The first peak of laying reflects activities of the large raptors, and the second peak is that of the insectivorous Burrowing Owl and Loggerhead Shrike. The peak for these two birds is most nearly coincident with that for grassland species, a category to which the Burrowing Owl might well be relegated.

Limnic Species

Six species, the Great Blue Heron, Green Heron, American Coot, American Avocet, Least Tern and Red-winged Blackbird, furnish

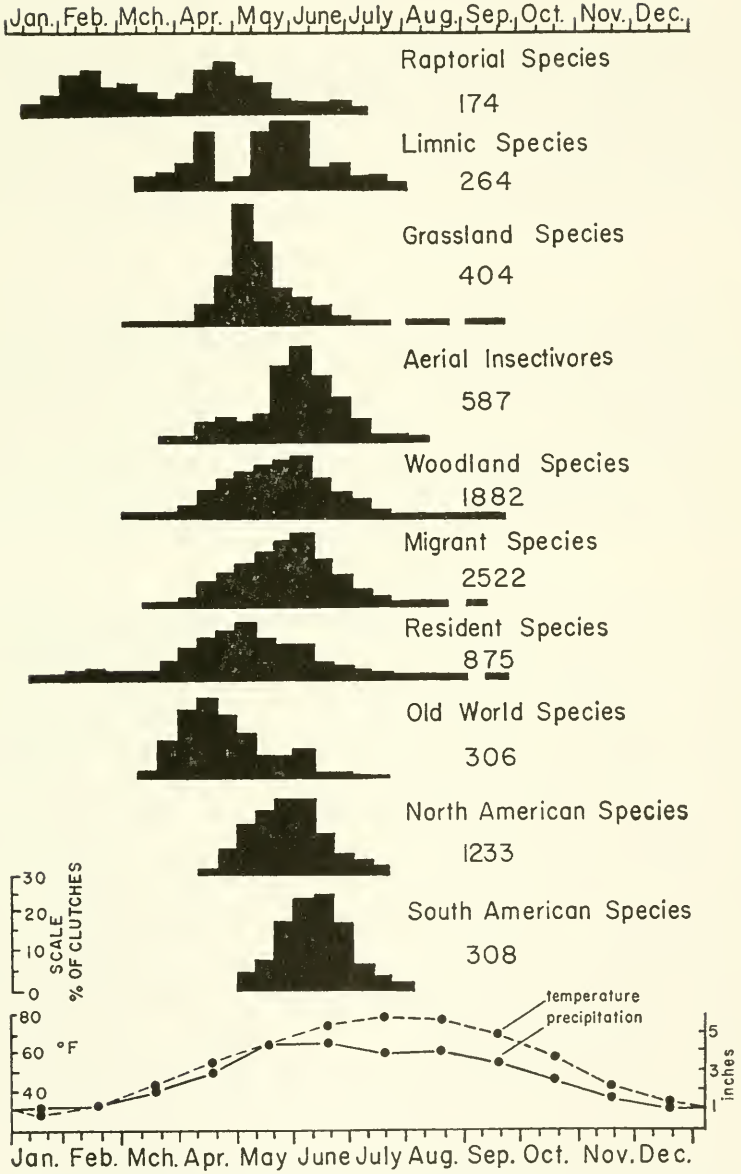

FIG. 1.—Histograms representing breeding schedules of ten categories of Kansan birds. Heights of columns indicate percentage of total of clutches of eggs, and widths indicate ten-day intervals of time, with the 5th, 15th, and 25th of each month as medians. The occurrences of monthly means of temperature and precipitation are indicated at the bottom of the figure.

264 records of breeding. The distribution of clutches (Fig. 1) runs from mid-March to the last third of July and is bimodal. This is another heterogeneous assemblage of birds; the Great Blue Heron is responsible for the first peak, in the first third of April. The other five species, however, show fair consistency and their peak of egg-laying almost coincides with peaks for aerial foragers, woodland species, and migrants, considered elsewhere in this section.

Grassland Species

Ten species, Greater Prairie Chicken, Bobwhite, Killdeer, Upland Plover, Horned Lark, Starling, Eastern Meadowlark, Western Meadowlark, Common Grackle, and Dickcissel, furnish 404 records of breeding activity. The distribution of clutches (Fig. 1) runs from the first of March to mid-September. The peak of egg-laying occurs in the first third of May. This is coincident with the peak for resident species, perhaps a reflection of the fact that half the species in the present category are residents in northeastern Kansas.

Woodland Species

In this category are included species characteristic of woodland edge. Thirty-four species, furnishing 1,882 records of breeding, are here treated: Yellow-billed Cuckoo, Black-billed Cuckoo, "flicker" (includes birds thought to be relatively pure red-shafted, pure yellow-shafted, as well as clear hybrids), Red-bellied Woodpecker, Red-headed Woodpecker, Hairy Woodpecker, Downy Woodpecker, Blue Jay, Black-billed Magpie, Common Crow, Black-capped Chickadee, Tufted Titmouse, Carolina Wren, Bewick Wren, House Wren, Brown Thrasher, Catbird, Mockingbird, Robin, Wood Thrush, Eastern Bluebird, Blue-gray Gnatcatcher, Bell Vireo, Warbling Vireo, Prothonotary Warbler, Yellow Warbler, Chat, Orchard Oriole, Baltimore Oriole, Cardinal, Black-headed Grosbeak, Indigo Bunting, Lark Sparrow, and Field Sparrow. The distribution of clutches runs from the first third of March to mid-September (Fig. 1). The modal period for completed clutches is the first third of June. Conspicuous breeding activity occurs from the first third of May to mid-June. The distribution of the season in time is almost identical with that for migrant species, reflecting the large number of migrant species in woodland habitats in Kansas.

Aerial Foragers

Twelve species, Common Nighthawk, Chimney Swift, Eastern Kingbird, Western Kingbird, Scissor-tailed Flycatcher, Great Crested Flycatcher, Eastern Phoebe, Eastern Wood Pewee, Bank

Swallow, Rough-winged Swallow, Barn Swallow, and Purple Martin, furnish 587 records of breeding. The distribution of clutches (Fig. 1) extends from the last third of March to the first third of August, and the modal date of clutches is in the first third of June. Conspicuous breeding activity occurs from the end of May to the end of June. The peak of nesting essentially coincides with that characteristic of migrants.

Zoogeographic Categories

Three categories of Mayr (1946) are of use in analyzing trends in breeding schedules of birds in Kansas. These categories of presumed ultimate evolutionary origin are the "Old World Element," the "North American Element," and the "South American Element." Not always have I agreed with Mayr's assignments of species to these categories, and such differences are noted. There is some obvious overlap between these categories and those discussed previously.

Old World Element

Eighteen species, Red-tailed Hawk, Rock Dove, Great Horned Owl, Hairy Woodpecker, Downy Woodpecker, Black-billed Magpie, Common Crow, Black-capped Chickadee, Tufted Titmouse, Robin, Loggerhead Shrike, Starling, House Sparrow, Bank Swallow, Barn Swallow, and Blue-gray Gnatcatcher, furnish 969 records of breeding (Fig. 1). Species for which I have records but which are not here listed are the Blue Jay and the Wood Thrush, both of which I consider to be better placed with the North American Element. The distribution of completed clutches runs from mid-January to the first third of August, and shows a tendency toward bimodality. The second, smaller peak is due to the inclusion of relatively large samples of three migrant species (Robin, Bank Swallow, and Barn Swallow). The timing of the breeding seasons of these three species is in every respect like that of most other migrants; if they are removed from the present sample the bimodality disappears, indicating an increase in homogeneity of the unit.

North American Element

Twenty-six species, Greater Prairie Chicken, Bobwhite, "flicker," Rough-winged Swallow, Purple Martin, Blue Jay, Carolina Wren, Bewick Wren, House Wren, Mockingbird, Catbird, Brown Thrasher, Wood Thrush, Bell Vireo, Warbling Vireo, Prothonotary Warbler, Yellow Warbler, Chat, Eastern Meadowlark, Western Meadowlark, Red-winged Blackbird, Orchard Oriole, Baltimore Oriole, Common

Grackle, Lark Sparrow, and Field Sparrow, furnish 1,233 records of breeding (Fig. 1). The distribution of completed clutches runs from the first third of April to the first third of September. The modal date for completion of clutches is June 1.

South American Element

Twelve species, Eastern Kingbird, Western Kingbird, Scissor-tailed Flycatcher, Great Crested Flycatcher, Yellow-bellied Flycatcher, Traill Flycatcher, Eastern Wood Pewee, Eastern Phoebe, Cardinal, Black-headed Grosbeak, Rose-breasted Grosbeak, and Indigo Bunting, furnish 552 records of breeding (Fig. 1). The curve representing this summary schedule is bimodal, wholly as a result of including the Eastern Phoebe and the Cardinal with this sample.

Relationship of Schedules to Temperature and Precipitation

In outlining the ten categories above, attention has been given to certain similarities and differences in the frequency distributions. A slightly more refined way of comparing the frequency distributions is to relate them to other, seasonally variable phenomena. Figure 1 shows the frequency distributions of egg-laying of these ten categories of birds in terms of the regular changes in mean temperature and mean precipitation characteristic of the environments in which these birds live in the breeding season.

Table 9 shows that there are two basic groups of birds according to peak of egg-laying and incidence of precipitation; raptors, birds of Eurasian origin, resident birds, and birds of grassland habitats tend to have their peaks of egg-laying prior to the peak of spring-summer rains, and the other six categories tend to have their peaks of egg-laying occur in the time of spring-summer rains. Regarding temperature, there are four categories of birds; these are evident in the table.

Some of the correspondences deserve comment. Residents and grassland species both breed before the rains come and before mean temperatures reach 70°F., and this correspondence probably results from most of the grassland species being residents. Contrariwise, most birds of Eurasian stocks are residents, but not all residents are of such stocks; the two groups are discrete when mean temperature at breeding is considered. Woodland birds, aerial foragers, and birds of South American evolutionary stocks breed after temperatures surpass 70°F. on the average. Almost all such species are migrants, but many migrants have different temporal characteristics, and the categories thus are shown to be discrete on the basis of temperature at time of breeding.

The change through spring and summer of temperature and precipitation delineates the inception and waxing of the growing season of vegetation and of the subsequent arthropod populations, on which most of the birds feed in the breeding season. The temporal characteristics of growing seasons in North America have been treated by Hopkins (1938) and have been related to timing of breeding seasons in Song Sparrows (*Passerella melodia*) of the Pacific coast of North America (Johnston, 1954).

Significance of Phylogeny to Breeding Schedules

Evidence from a variety of sources demonstrates that timing of breeding seasons is either broadly or specifically genetically-determined. For some species in some situations major environmental variables are paramount in regulating timing of breeding, but in others the innate, regulatory "clock" is less closely tied to conspicuous exogenous stimuli. The work by Miller (1955a, 1955b, 1960) with several species of *Zonotrichia* strongly indicates that endogenous timing is most important for these birds, and there is ecological evidence for Song Sparrows that supports the same point (Johnston, 1954, 1956). It is, in any event, possible to treat breeding schedules as species-specific characters, for any one geographic area.

In an attempt to relate a breeding schedule to previous ancestral modes, that is by extension to phylogeny, it is necessary to know how often ancestral adaptations can persist in the face of necessity to adapt to present environmental conditions. It is necessary to know how conservative or how immediately plastic breeding schedules can be. The disadvantage of using available information about configurations of breeding seasons (as shown in Figs. 3 to 9) is that it is extremely difficult to compare visually at one time more than six or eight histograms as to the trenchant similarities and differences regarding times of inception and cessation of breeding, and time of peak egg-laying. It is possible, however, to reduce these three variables to one variable (as described below), which allows the necessary comparisons to be made more easily; this variable may be called the *breeding index.*

Calculation of Breeding Index

The chronological year is broken roughly into ten-day intervals numbered 1 to 36. The histogram describing the temporal occurrence of the breeding season of a species in our area usually will lie within intervals 7 to 25. The modal date for completion of clutches is given a value corresponding to the number of ten-day

intervals beyond interval 7 (March 1-10); this describes the modal variable. The date of completion of 83 per cent of all clutches is given a value corresponding to the number of ten-day intervals it lies from interval 11 (April 11-20); this describes the 83 per cent variable (and is a measure of the length of the season in terms of its inception). The breeding index can then be calculated as follows:

$$I = x_m + x_{sd},$$

where: I is the breeding index,
x_m is the modal variable, and
x_{sd} is the 83 per cent variable.

This is obviously an arbitrary scheme to gain a simple measure of beginning, peak, and end of a breeding season. Other schemes could be devised whereby different absolute values would be involved, but the relative nature of the results would be preserved. The values under the present system for 73 species of Kansan birds run from -5 to $+22$; early modal dates and cessation to breeding give low values, late dates high values.

Within this framework there are other, presumably subordinate, factors that influence the values of breeding indices, as follows:

1. Migratory habit. Any migrant tends to arrive on breeding grounds relatively late, hence migrants ordinarily have higher index values than do residents.

2. Colonial breeding. The strong synchrony of colonially-breeding species tends to move the modal egg-date toward the time of inception of breeding; as a result colonially-breeding species probably have lower index values than they would have if not colonial.

3. Single-broodedness. Species having only one brood per season tend to have shorter seasons than double-brooded species, and their index values tend to be lower than those of double-brooded species.

Migratory habit unquestionably has considerable influence on index values in some species. It is not, however, as important as other matters, such as the condition of the food substratum or sensitivity of the pituitary-gonadal mechanism, in determining timing and mode of breeding activity. The schedule of the Purple Martin is the extreme example showing that time of spring arrival on breeding grounds is not necessarily related to time of inception of breeding. It should be emphasized that the factors leading to northward migratory movement may be involved in timing of the annual gonadal and reproductive cycle.

Figure 2 presents a graphic summary of values of breeding

FIG. 2.—Breeding indices for Kansan birds. Vertical hash-marks indicate the value of breeding index for a given species; horizontal lines show the range of values of breeding index for families and orders.

indices for many groups of Kansan birds. The values for species of a given family have been linked by a horizontal line. The length of this line is proportional to the degree to which the index values for the species concerned resemble one another. Note that the plottings for the Picidae, Corvidae, Turdidae, Tyrannidae, and Icteridae each contain one point that is well-removed from a cluster of points. This can be interpreted as a measure of the frequency of adaptive plasticity versus adaptive conservatism; five of the 24 plottings show a plastic character, 19 a conservative. There are 26 plottings that show temporal consistency, all of which may be taken as evidence of adaptive (or relictual) conservatism of the species in question.

Conclusion

Such patterns of breeding chronology support the idea that seasonal response to the necessities of breeding is conservative more often than plastic. Most students of breeding schedules believe that since these are highly adaptive, they must also be capable of flexibility to meet variable environments within the range of the species. Such thinking receives support when different geographic localities are considered for one species (Johnston, 1954), or when specific features of a special environment are considered (see Miller, 1960; Johnston, 1956).

Yet, if one, relatively restricted locality is considered, as in the present study, evidence of a conservative characteristic in breeding schedules can be detected. This conservatism may result from the historic genetic "burden" of the species; that is to say, previous adaptive peaks may in part be evident in the matrix of contemporary adaptation. Adaptive relicts of morphological nature have been many times documented, but characteristics associated with seasonality and timing schedules have not.

In any event, genetic relationships are evident in the configuration of breeding seasons of many species here treated. Thus, any consideration of variation in breeding schedules must be sensitive to the limits, whether broad or restricting, that the heritage of a species sets on its present chronological adaptation.

Regulation of Breeding Schedules

Regulation of breeding schedules in birds always involves some exogenous, environmental timing or triggering mechanism. Broad limits to functional reproductive activity seem to be set by the photoperiod-neuroendocrine system. This basic, predominately extra-equatorial, regulator can be ignored by temperate-zone species only if they possess chronological adaptation to special, aperiodic environmental conditions, as does the Red Crossbill (*Loxia curvirostra;* see McCabe and McCabe, 1933; H. B. Tordoff, ms.), for which the chief consideration seems to be availability of conifer seeds. Environmental phonomena otherwise known to trigger breeding activity include rainfall (Davis, 1953; Williamson, 1956), presence of suitable nesting material (Marshall and Disney, 1957; Lehrman, 1958), temperature (Nice, 1937), and presence of a mate (Lehrman, Brody, and Wortis, 1961). Such regulators, or environmental oscillators, are the "phasing factors" of the physiologic clock that dictate the temporal occurrence of primary reproductive activity.

TABLE 9.—RELATIONSHIP BETWEEN ENVIRONMENTAL FACTORS AND TIMING OF BREEDING IN BIRDS OF KANSAS

	Occurrence of Peak of Egg-laying					
	When Precipitation is:		When Mean Temperature (F.) is:			
	Light	Heavy	< 55°	< 70°	± 70°	> 70°
Raptors	x		x			
O.W. Element	x		x			
Residents	x			x		
Grassland species	x			x		
Marshland species		x			x	
N. Amer. Element		x			x	
Migrants		x			x	
Woodland species		x				x
Aerial foragers		x				x
S. Amer. Element		x				x

None of the regulators mentioned above has been specifically investigated for any Kansan bird, but it is reasonable to suppose that, in these temperate-zone species, the photoperiod is the most important general phasing factor in seasonal breeding. Although gonadal response and seasonal restriction of breeding are set by the photoperiod, specific temporal relationships are dictated by more immediate environmental variables.

Table 9, as already noted, shows the gross relationships between certain groups of birds, certain arbitrary indicators of seasonal temperature-humidity conditions bearing significantly on the growing season, and occurrence in time of peak of egg-laying by the birds involved. Some species and groups of Kansan birds breed chiefly under cool-dry environmental conditions, and some under warm-wet environmental conditions. Within each of these categories some variation occurs. Thus, raptors and boreally-adapted species (the Eurasian zoogeographic element) breed under cool conditions prior to rains, and residents and grassland species breed under slightly warmer conditions prior to rains; limnic species, species derived from North American evolutionary stocks, and migrants tend to breed in the cooler segment of the warm-wet period, and woodland birds, aerial foragers, and species derived from South American evolutionary stocks tend to breed in the warmer segment of the warm-wet period.

So much, then, for relationships between birds and their environments at a descriptive level. It would be useful at this point to

examine how environmental variables relate to timing of breeding. Certain independent lines of investigation indicate that birds have a well-developed internal timing device; most convincing is the work of Schmidt-Koenig (1960) and the others who have shown that the endogenous clock of birds can be shifted in its periodicity forward or backward in time. This and much other evidence (see Brown, 1960) indicate that many fundamental periodic regulators are extrinsic to the animal; it is thus permissible for present purposes to consider any expression of variation in timing as dependent on environmental oscillators. It is not hereby meant to ignore the fact that differential responses to dominant environmental variables occur within a species, indicating endogenous control over timing of breeding. The work by Miller (1960:518) with three populations of the White-crowned Sparrow, revealing innately different responses to vernal photoperiodic increase, is especially important in this regard. For the moment, however, we may consider exogenous controls only.

Any exogenous control, or environmental variable, can be looked on simply as a timing oscillator. Such variables show regular or irregular periodic activity, and the independent actions as a whole result in the more-or-less variable annual schedule of breeding for any species at any one place. It would seem that some oscillators are linked to one another, but there is a real question concerning the over-all degree to which linkage is present. It is significant that frequency distributions of breeding activity of various species and groups of birds take on the shape of a skewed normal curve. The more information is added to such distributions, the more nearly they approach being wholly normal, with irregularities tending to disappear. This kind of response itself is evidence that most of the variables influencing the distribution are not mutually linked.

This conclusion is warranted if we examine what would happen to frequency distributions if the variables or oscillators regulating timing were linked. The frequency distribution of breeding activity in birds is described by a nonlinear curve (a normal distribution is nonlinear). Let us assume that each of the environmental variables is a nonlinear oscillator, as is probable. A set of nonlinear oscillators mutually entrained or coupled and operating with reference to a given phenomenon would result in that phenomenon being described by a frequency distribution much more stable than if it were regulated by any one oscillator alone. However, the frequency distribution of a set of coupled nonlinear oscillators is non-normal (Wiener, 1958).

We do not obtain such distributions in describing breeding activity, so we may say that the oscillators regulating such activity are not coupled. Present distribution, habitat preference, residency status, foraging adaptation, previous zoogeographic history, and relicts of ancestral adaptation, all bear on the character of the breeding schedule of any bird species. The emphasis above on multiple regulation of breeding schedules conceivably reflects the true picture, but any such emphasis is made at the expense of taking one factor as basic, or reducing the many to one, in order to manufacture simplicity.

ACCOUNTS OF SPECIES

In each account below information is given concerning status, habitat, geographic distribution, seasonal occurrence, schedule of egg-laying, number of eggs laid, and sites of nests, as these pertain to Kansas, unless otherwise stated. The ways in which some of these points were elucidated are as follows.

1.—Breeding schedule. Frequency distributions of egg-laying in time are calculated on the basis of dates of completed clutches, as described earlier (p. 588). Any event in the series of actions of nesting—nestbuilding, egg-laying incubation, brooding, feeding young out of nests—can be manipulated by adding or subtracting days to or from the date of record to yield the probable date of completion of the clutch. The resulting data are grouped into class intervals of ten days. Extreme dates here given for egg-laying may be as much as nine days off in accuracy, but the error does not often exceed five days. Extreme dates indicated here may be taken as actual or predicted extremes. The raw data used are on file at the Museum of Natural History and are available for use by any qualified individual.

2.—Dates of occurrence. First and last annual occurrences in the State for migrant species are indicated by both a range of dates and a median date. Twenty to 30 dates of first observation in spring are available for most of the common species, and 10 to 20 dates of last observation in autumn are at hand for such species. The median dates, earlier than and subsequent to which an equal number of observations are available, are reliable indicators of the dates on which a species is likely to be seen first in the State in an average year.

3.—Clutch-size. Information on number of eggs is given for each species according to the mode, followed by the mean, the range, and the size of the sample.

4.—Distribution in Kansas. Information on distribution in the

breeding season within the borders of Kansas is given in accounts below chiefly by reference to one or more counties of the State. Location of counties can be made by referring to Figure 10.

Pied-billed Grebe: *Podilymbus podiceps podiceps* (Linnaeus).—This is a common but local summer resident, in and on ponds, marshes, streams, ditches, and lakes. The species can be seen in the State at any time, but usually arrives in the period March 1 to April 13 (the median is March 21), and departs southward in the period October 13 to November 18 (the median is October 24).

Breeding schedule.—Nineteen records of breeding span the period May 1 to June 30; the modal date for egg-laying is May 15.

Number of eggs.—Clutch-size is 4 to 10 eggs.

Nests are floating masses of marsh vegetation (cattail, smartweed, duckweed, filamentous green algae, and the like), kept green on top by addition of fresh material, in or at the edge of emergent marsh vegetation.

Double-crested Cormorant: *Phalacrocorax auritus auritus* (Lesson).—This is a transient, but has been found nesting on one occasion in Barton County (Tordoff, 1956:311).

Breeding schedule.—Eggs were laid in July and August in the one known nesting effort.

Number of eggs.—Clutch-size is 2 to 4 eggs (Davie, 1898).

Great Blue Heron: *Ardea herodias* Linnaeus.—This common summer resident nests in tall trees along rivers, streams, and marshes. The sector of greatest abundance is the Flint Hills. *A. h. herodias* Linnaeus occurs in extreme northeastern Kansas, *A. h. wardi* Ridgway breeds in southeastern Kansas, and *A. h. treganzai* Court breeds in western Kansas; specimens showing intermediate morphology have been taken from the central part of the State. Occurrence in time, exclusive of the few that overwinter in Kansas, is shown in Table 10.

Breeding schedule.—Seventy-seven records of breeding span the period March 1 to April 30 (Fig. 3); the modal date of egg-laying is April 5.

Number of eggs.—Clutch-size is 4 eggs (4.4, 3-6; 36).

TABLE 10.—OCCURRENCE IN TIME OF SUMMER RESIDENT HERONS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Great Blue Heron	Feb. 4–Apr. 8	Mar. 20	Oct. 10–Nov. 29	Oct. 23
Green Heron	Mar. 29–May 4	Apr. 27	Sept. 1–Oct. 30	Sept. 9
Common Egret	Apr. 8–May 12	Apr. 2	Sept. 4–Sept. 30	Sept. 21
Black-crowned Night Heron	Mar. 27–May 18	Apr. 25	Sept. 10–Nov. 11	Sept. 25
Yellow-crowned Night Heron	Apr. 15–May 18	Apr. 27	.....	.....
American Bittern	Apr. 4–May 9	May 1	Oct. 6–Dec. 12	Oct. 16
Least Bittern	Apr. 9–May 22	Apr. 8	Oct. 24	.....

Nests are placed in crotches of sycamore, cottonwood, elm, hackberry, oak, and walnut, from 30 to 60 feet high; the average height is about 40 feet.

Green Heron: *Butorides virescens virescens* (Linnaeus).—This is a common summer resident about streams, lakes, and marshes throughout the State. Some characteristics of the temporal occurrence of this species are indicated in Table 10.

Breeding schedule.—Twenty-eight records of breeding span the period April 21 to June 20 (Fig. 3); the modal date of completion of clutches is May 5.

Number of eggs.—Clutch-size is 3 eggs (3.1, 3-5; 17).

Nests are placed about 10 feet high (two to 35 feet) in willow, cottonwood, elm, and the like.

Little Blue Heron: *Florida caerulea caerulea* (Linnaeus).—This is chiefly a postbreeding summer visitant, but there is one record of breeding in Finney County (Tordoff, 1956:312).

Breeding schedule.—There is no information on breeding schedule in Kansas or in adjacent areas.

Number of eggs.—Clutch-size is 2 to 4 eggs (Davie, 1898).

Nests are placed in trees and bushes at various heights above the ground.

Common Egret: *Casmerodius albus egretta* (Gmelin).—This is a postbreeding summer visitant, but has been found nesting once in Cowley County (Johnston, 1960:10). Occurrence in time is listed in Table 10.

Breeding schedule.—There is no information on breeding schedule in Kansas.

Number of eggs.—Clutch-size is 2 to 4 eggs (Davie, 1898).

Nests are placed in trees, usually above 20 feet in height; the one instance of nesting in the State was within a colony of Great Blue Herons.

Snowy Egret: *Leucophoyx thula thula* (Molina).—This postbreeding summer visitant has been found nesting once in Finney County (Tordoff, 1956:312).

Breeding schedule.—There is no information on breeding schedule in the State.

Number of eggs.—Clutch-size is 2 to 5 eggs (Davie, 1898).

Nests in Kansas are placed among those of Great Blue Herons.

Black-crowned Night Heron: *Nycticorax nycticorax hoactli* (Gmelin).—This is a locally common summer resident around marshes and riparian habitats. Characteristics of the occurrence of the species in time are given in Table 10.

Breeding schedule.—Eggs are laid in the period May 1 to August 10.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed at medium elevations in riparian trees, in Kansas chiefly cottonwood, or in beds of emergent marsh vegetation.

Yellow-crowned Night Heron: *Nyctanassa violacea violacea* (Linnaeus).—This is a local summer resident in riparian habitats, chiefly in southeastern Kansas. Specimens taken in the breeding season and records of nesting come from Meade, Stafford, Doniphan, Douglas, Greenwood, Woodson, Labette, and Cherokee counties. Characteristics of occurrence in time in Kansas are shown in Table 10.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed in riparian trees.

Least Bittern: *Ixobrychus exilis exilis* (Gmelin).—This is a local summer resident in marshland. Characteristics of its occurrence in time are indicated in Table 10.

Breeding schedule.—Eleven records of breeding span the period May 21 to July 20; the modal date of egg-laying seems to be in the first week of June.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed in dense emergent vegetation a few inches to a foot above the surface of the water.

American Bittern: *Botaurus lentiginosus* (Rackett).—This is a local summer resident in marshes and heavy grassland. The species occurs temporally according to characteristics as listed in Table 10.

Breeding schedule.—Eggs are laid in May and probably in June.

Number of eggs.—Clutch-size is 3 or 4 eggs.

Nests are placed on the ground in heavy cover.

White-faced Ibis: *Plegadis chihi* (Vieillot).—This is a local summer resident in marshland; actual records of breeding come only from Barton County (Nossaman, 1952:7; Zuvanich, 1963; M. Schwilling, personal communication, July, 1962). The species has been recorded in the State from April 17 to October 6.

Breeding schedule.—Twenty-five breeding records are for June and early July.

Number of eggs.—Clutch-size is about 4 eggs (3.9, 3-4; 24).

Nests are placed in emergent marsh vegetation near the surface of the water, in Barton County in extensive cattail beds harboring also Black-crowned Night Herons.

Mallard: *Anas platyrhynchos platyrhynchos* Linnaeus.—This is a local summer resident around marshes. The time of greatest abundance is October to April, but most birds move north for breeding.

Breeding schedule.—Fifteen records of breeding span the period April 1 to June 10; the modal date of egg-laying is in the first ten days of May.

Number of eggs.—Clutch-size varies widely; first clutches are of about 12 eggs. Brood sizes vary from 3 to 12 individuals in Kansas.

Nests are placed on the ground surface, in pasture grasses, marsh grasses, cattail, sedge, and smartweed.

Pintail: *Anas acuta* Linnaeus.—This is a local summer resident in marshland. The time of greatest abundance is from September to May, but most birds move north for breeding.

Breeding schedule.—Eleven records of breeding span the period April 21 to June 10; the peak of egg-laying seems to be in the period May 1 to 10.

Number of eggs.—Clutch-size is around 10 eggs. Brood sizes vary from 3 to 8 individuals in Kansas.

Nests are placed on the ground surface, in cover of marsh grass, cattail, or sedge.

Blue-winged Teal: *Anas discors discors* Linnaeus.—This summer resident is locally common around marshes and ponds. The species arrives in spring in the period March 9 to April 5 (the median is March 23); birds are last seen sometime between October 7 and November 26 (the median is October 20).

Breeding schedule.—Twenty-two records of breeding span the period May 1 to May 30; the peak of egg-laying is around May 15. It is doubtful that the present data indicate the full extent of the egg-season in this duck.

Number of eggs.—Clutch-size is 8 to 12 eggs.

Nests are placed on the ground surface, in cover of grasses, cattail and sedges.

Shoveler: *Anas clypeata* Linnaeus.—This is an irregular and local summer resident, around marshes. Most individuals seen in the State are passage migrants. Breeding records are from Barton and Finney counties.

Breeding schedule.—Seasonal limits are unknown for the Shoveler in Kansas.

Number of eggs.—Clutch-size is about 8 eggs (Davie, 1898).

Nests are placed on the ground surface in cover of marsh vegetation.

Wood Duck: *Aix sponsa* (Linnaeus).—This is an uncommon summer resident around wooded streams and ponds in eastern Kansas. Nesting records and specimens taken in the breeding season come from east of stations in Pottawatomie, Coffey, and Woodson counties. Most nesting records at present come from the Marais des Cygnes Wildlife Refuge, Linn County. The species is present in the State from March 5 to December 8.

Breeding schedule.—Eleven records of breeding span the period March 21 to May 10; the peak of egg-laying is probably in mid-April. The present data are inadequate for showing the full span of the breeding season.

Number of eggs.—Clutch-size is around 15 eggs, varying from 10 to 23 in the sample at hand.

Nests are placed in crevices and hollows in trees near water, 10 to 70 feet high.

Redhead: *Aythya americana* (Eyton).—This duck nested at Cheyenne Bottoms, Barton County, 1962: 9 eggs found May 31 (M. Schwilling); also reported to have nested at Cheyenne Bottoms about 1928 (Tordoff, 1956:316).

Canvasback: *Aythya valisineria* (Wilson).—This duck nested at Cheyenne Bottoms, Barton County, 1962: 14 eggs found June 20 (M. Schwilling).

Ruddy Duck: *Oxyura jamaicensis rubida* (Wilson).—This is a local summer resident in marshland; numbers seem generally higher in western than in eastern Kansas. The season of greatest abundance is March through November, but numbers are conspicuously reduced in midsummer.

Breeding schedule.—Eggs are known to be laid in May and June.

Number of eggs.—Clutch-size is about 10 eggs (Davie, 1898).

Nests are placed near the edge of water, either in or on emergent marsh vegetation; nests of other marshland birds, such as coots, are sometimes appropriated (Davie, 1898).

Turkey Vulture: *Cathartes aura teter* Friedmann.—This summer resident is common throughout Kansas. Occurrence in time is indicated in Table 11.

Breeding schedule.—Fifteen records of breeding span the period April 21

to June 10; earlier records will doubtless be found, to judge from the frequency distribution of the present sample. The peak of egg-laying is perhaps around May 1.

Number of eggs.—Clutch-size is 2 eggs (1.8, 1-2; 12).

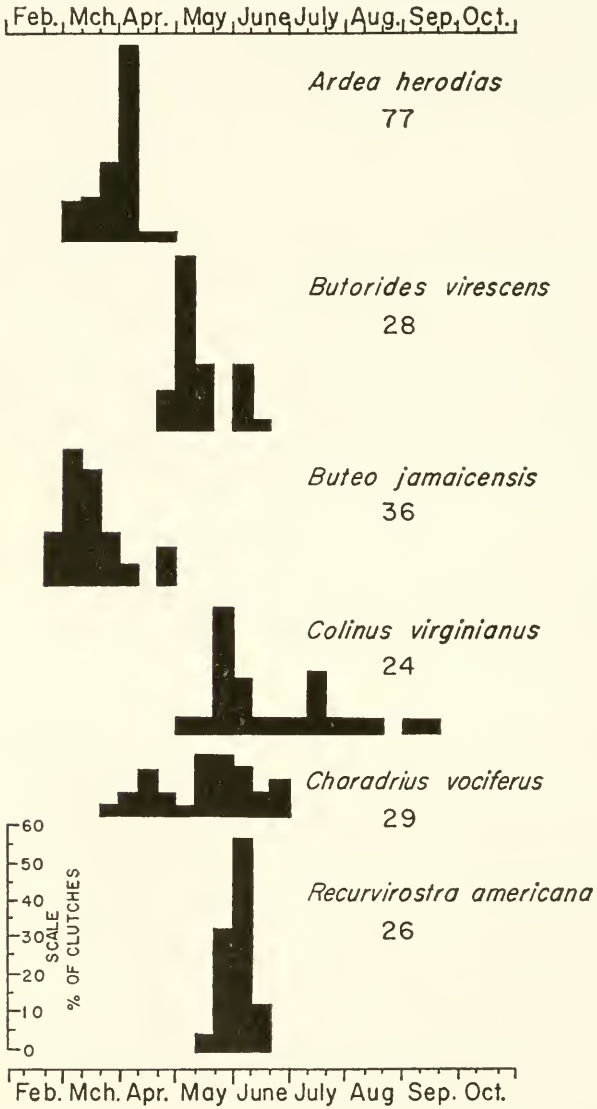

FIG. 3.—Histograms representing breeding schedules of two herons, the Red-tailed Hawk, Bobwhite, and two shore birds in Kansas. See legend to Figure 1 for explanation of histograms.

Nests are placed in holes and crevices in trees and cliffs, on rocky ledges, and the like.

Black Vulture: *Coragyps atratus* (Meyer).—This is possibly a summer resident in the southeastern sector of Kansas. There is one nesting record, for Labette County (Goss, 1891:245).

Breeding schedule.—There are no data for this species in Kansas.

Number of eggs.—Clutch-size is 2 eggs (Davie, 1898).

Nests are placed in hollows (logs, stumps, *etc.*) on the ground surface.

Swallow-tailed Kite: *Elanoides forficatus forficatus* (Linnaeus).—This kite was formerly a summer resident in eastern Kansas; it no longer occurs as a breeding species.

Breeding schedule.—In Kansas the season seemed to occur relatively late in the year for a raptor; eggs were laid in May, so far as is known.

Number of eggs.—Clutch-size is about 2 eggs (Davie, 1898).

Nests are placed in tops of trees.

Mississippi Kite: *Ictinia misisippiensis* (Wilson).—This is a common summer resident in southern Kansas, west to Morton County. Specimens taken in the breeding season and records of nesting come from south of stations in Grant, Barton, Harvey, and Douglas counties; the present center of abundance is in Meade, Clark, Comanche, Barber, and Harper counties.

Breeding schedule.—Seven records of breeding span the period April 20 to June 10; the peak of egg-laying seems to be in the first week of May.

Number of eggs.—Clutch-size is 2 eggs.

Nests are placed about 35 feet high (from 25 to 50 feet) in cottonwood, willow, elm, black locust, and the like.

Sharp-shinned Hawk: *Accipiter striatus velox* (Wilson).—This rare summer resident apparently occurs only in the eastern part. The two nesting records are from Cloud and Pottawatomie counties.

Breeding schedule.—The information at hand suggests the birds lay in April and May.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898).

Nests are placed 20 or more feet high in coniferous or deciduous trees.

Cooper Hawk: *Accipiter cooperii* (Bonaparte).—This is an uncommon resident. Specimens taken in the breeding season and actual records of nesting come from east of stations in Cloud, Anderson, and Montgomery counties.

Breeding schedule.—Fourteen records of breeding span the period March 21 to May 30; the modal date of egg-laying is April 25.

Number of eggs.—Clutch-size is 4 eggs (3.8, 2-5; 5).

Nests are placed from 15 to 30 feet high, averaging 25 feet in elm, oak, and other trees.

Red-tailed Hawk: *Buteo jamaicensis borealis* (Gmelin).—This is a common resident east of the 100th meridian; to the west numbers are reduced, although the species is by no means unusual in western Kansas. Red-tails probably always were uncommon in western Kansas; Wolfe (1961) reports that they were "very rare as a nesting species" in Decatur County shortly after the turn of the 20th Century.

Breeding schedule.—Thirty-six records of breeding span the period February 21 to April 10 (Fig. 3); the modal date of egg-laying is March 5.

Number of eggs.—Clutch-size is 3 eggs (2.6, 2-3; 20).

Nests are placed about 40 feet high, ranging from 15 to 70 feet in cottonwood, honey locust, osage orange, sycamore, and walnut.

Red-shouldered Hawk: *Buteo lineatus lineatus* (Gmelin).—This is an uncommon summer resident in eastern Kansas, in riparian and bottomland timber. Nesting records are available from Leavenworth, Woodson, and Linn counties, and red-shoulders probably also nest in Doniphan County (Linsdale, 1928).

Breeding season.—Eggs are laid in March and April.

Number of eggs.—Clutch-size is about 3 eggs (Davie, 1898).

Nests are placed up to 70 feet high in elms and other streamside trees.

TABLE 11.—OCCURRENCE IN TIME OF THE SUMMER RESIDENT VULTURE AND HAWKS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Turkey Vulture....	Mar. 7–Mar. 30	Mar. 15	Sept. 24–Oct. 28	Oct. 5
Red-shouldered Hawk.....	Feb. 10–Mar. 14	Feb. 26	Oct.–Dec.	.....
Broad-winged Hawk.....	Apr. 4–Apr. 21	Apr. 12	Sept. 1–Oct. 20	.....
Swainson Hawk....	Mar. 24–Apr. 28	Apr. 12	Oct. 5–Nov. 2	Oct. 11

Broad-winged Hawk: *Buteo platypterus platypterus* (Vieillot).—This is an uncommon summer resident in eastern Kansas, in swampy woodland. Specimens taken in the breeding season and nesting records are from Shawnee, Douglas, Leavenworth, and Johnson counties; there are several nesting records from Missouri in the bottomlands just across the river from Wyandotte County Kansas. Occurrence in time is listed in Table 11.

Breeding schedule.—Four records of nesting span the period April 21 to May 30, but it is likely that the egg-season is longer than this.

Number of eggs.—Clutch-size is about 3 eggs.

Nests are placed high in deciduous trees.

Swainson Hawk: *Buteo swainsoni* Bonaparte.—This is a common summer resident in prairie grassland with open groves and scattered trees. Records of breeding are available from all parts of the State, but are least numerous from the southeastern quarter. Occurrence in time is listed in Table 11.

Breeding schedule.—Sixteen records of breeding span the period April 11 to June 10; the modal date for completion of clutches is April 25.

Number of eggs.—Clutch-size is 2 eggs (2.4, 2-3; 5).

Nests are placed about 35 feet high, actually ranging from 12 to 75 feet, in cottonwood, elm, willow, and honey locust. Occasionally nests are placed on ledges in cliffs.

Ferruginous Hawk: *Buteo regalis* (Gray).—This is an uncommon resident in western Kansas, in grassland with scattered trees. Records of nesting and specimens taken in the breeding season come from Wallace, Hamilton, Gove, Logan, and Finney counties.

Breeding schedule.—Five records of breeding span the period March 11 to April 30.

Number of eggs.—Clutch-size is about 3 eggs (3.3, 3-4; 4).

Nests are placed on the ground surface on small cliffs or promontories or low (six to 10 feet) in small trees such as osage orange, cottonwood, and mulberry.

Marsh Hawk: *Circus cyaneus hudsonius* (Linnaeus).—This is a local resident in grassland throughout Kansas. Most records of breeding come from east of the Flint Hills, but it is not certain that the few records from the west actually reflect a low density of Marsh Hawks in that area.

Breeding schedule.—Sixteen records of breeding span the period April 11 to May 20; the modal date for egg-laying is May 5.

Number of eggs.—Clutch-size is 5 eggs (5.2, 3-7; 14).

Nests are placed on the ground surface in grassy cover.

Peregrine Falcon: *Falco peregrinus anatum* Bonaparte.—This falcon nested, perhaps regularly but clearly in small numbers, in Kansas prior to the 20th Century. The best documented breeding occurrence was at Neosho Falls, Woodson County (Goss, 1891:283).

Breeding schedule.—Eggs were recorded as being laid in February and March.

Number of eggs.—Clutch-size is 3 or 4 eggs (Davie, 1898).

Nests are placed relatively high on cliffs and in trees; at Neosho Falls these birds used open cavities 50 to 60 feet high in sycamores.

Sparrow Hawk: *Falco sparverius sparverius* Linnaeus.—This is a common resident throughout Kansas, in parkland and woodland edge.

Breeding schedule.—Thirteen records of egg-laying span the period March 21 to May 20; the modal date of laying is not evident in this sample but it probably falls around April 10.

Number of eggs.—Clutch-size is 4 eggs (4.2, 3-5; 5).

Nests are placed in cavities about 16 feet high, actually 12 to 30 feet, in cottonwood, ash, maple, Purple Martin "houses," and human dwellings.

Greater Prairie Chicken: *Tympanuchus cupido pinnatus* (Brewster).—This is a locally common resident in eastern Kansas, in and about bluestem prairie grassland, and is local in the northwest in undisturbed plains grassland. Wolfe (1961) reports that the species was common in Decatur County shortly after the turn of the Century, but that it became rare by 1914.

Breeding schedule.—Twenty-one records of breeding span the period May 1 to June 10 (Fig. 3); the modal date for laying is May 5. The sample indicates an abrupt inception to laying of eggs, and this may be a reflection of timing characteristic of behavior at leks, or booming grounds.

Number of eggs.—Clutch-size is 12 eggs (11.7, 9-15; 17).

Nests are placed on the surface of the ground in bluestem grassland or plains bunchgrass, usually under cover of prairie grasses and forbs.

Lesser Prairie Chicken: *Tympanuchus pallidicinctus* (Ridgway).—This is a local resident in sandy grassland in southwestern Kansas. Distribution is to the west and south of Pawnee County.

Breeding schedule.—There is no information on timing of the breeding season in Kansas.

Number of eggs.—Clutch-size is thought to be near that of the Greater Prairie Chicken. Vic Housholder (MS) observed a hen with ten chicks ten miles south of Dodge City, Ford County, on June 1, 1955.

Bobwhite: *Colinus virginianus* (Linnaeus).—This is a common resident in the east, but is local in western Kansas; occurrence is in broken woodland and other edge habitats. *C. v. virginianus* (Linnaeus) is found northeast of stations in Nemaha, Douglas, and Miami counties, and *C. v. taylori* Lincoln is found in the remainder of the State.

Breeding schedule.—Twenty-four records of breeding span the period May 1 to September 20 (Fig. 3); the modal date for first clutches is May 25. The long period of egg-laying after May probably includes both renesting efforts and true second nestings.

Number of eggs.—Clutch-size is about 13 eggs (12.8, 8-21; 22); in the present sample 16 eggs was the most frequent number.

Nests are placed on the surface of the ground at bases of bunch grasses, saplings, trees, or posts, under cover of prairie grasses, forbs, or small woody plants.

Scaled Quail: *Callipepla squamata pallida* Brewster.—This is a locally common resident in southwestern Kansas, chiefly west of Clark County and south of the Arkansas River; preferred habitat seems to be in open, sandy prairie.

Breeding schedule.—Eggs are laid at least in May; the egg-season in Kansas is unlikely to be so prolonged as that of the Bobwhite; among other factors involved, the Scaled Quail in Kansas is at a northern extreme of its distribution, where suboptimal environmental conditions may occur relatively frequently.

Number of eggs.—Clutch-size is around 10 to 12 eggs.

Nests are placed on the ground surface under woody or herbaceous cover.

Ring-necked Pheasant: *Phasianus colchicus* Linnaeus.—This introduced resident is common in western Kansas, is local and uncommon in the east, and is found in agricultural land with scattered woody vegetation.

Breeding schedule.—Eggs are laid at least in May.

Number of eggs.—Clutch-size is 10 to 12 eggs.

Nests are placed on the surface of the ground in woody or herbaceous cover.

Wild Turkey: *Meleagris gallopavo* Linnaeus.—Turkeys formerly occurred as common residents in floodplain woodland in eastern Kansas, and their distribution extended through the west in riparian woodland. Present population in eastern and southern sectors are partly the result of introductions of birds from Missouri by humans in the 1950s. Turkeys in southern Kansas are also present owing to natural dispersal along the Arkansas and Medicine Lodge rivers of birds native to and introduced into Oklahoma. No specimens of turkeys presently found in Kansas are available for examination but these birds

probably are referable to *M. g. silvestris* Vieillot, the trinomen applied to turkeys in Missouri and northeastern Oklahoma.

Turkeys from southern Texas recently have been liberated at several localities in southern Nebraska; turkeys seen in extreme northern Kansas are thus probably of these stocks. The name *M. g. intermedia* Sennett is applicable to these birds.

Breeding schedule.—No information is available on the egg-season in Kansas; turkeys have nested in southern Kansas within recent years, however.

Number of eggs.—Clutch-size is perhaps 12 eggs.

Nests are placed on the surface of the ground, usually well-concealed under woody vegetation.

King Rail: *Rallus elegans elegans* Audubon.—This summer resident is locally common in marshlands. Nesting records or adults taken in the breeding season are from Cheyenne, Meade, Pratt, Stafford, Cloud, Riley, Douglas, Anderson, and Allen counties. Dates of arrival in spring are recorded from April 7 to April 28; the median date is April 18. Departure in autumn is possibly as early as September in the north, but four records are in the period October 12 to November 25. The species occasionally can be found in winter (Douglas County, December 28, 1915).

Breeding schedule.—Fourteen records of breeding span the period May 1 to July 20; the modal date for egg-laying is June 5.

Number of eggs.—Clutch-size is about 10 eggs (9 to 12; 4 records).

Nests are placed on the surface of the ground, under grassy or woody cover.

Virginia Rail: *Rallus limicola limicola Vieillot.*—This is an uncommon summer resident, presumably throughout the State. The one breeding record is from Morton County (May 24, 1950; Graber and Graber, 1951). Dates of spring arrival are from April 19 to May 18; dates of last observation in autumn are within the period September 1 to October 30. A few birds overwinter in the southern part of the State (Meade County, December and January).

Breeding season.—Eggs are laid probably in May and June.

Number of eggs.—Six to 12 eggs are laid (Davie, 1898).

Nests are placed in emergent aquatic plants, near the surface of the water.

Sora: *Porzana carolina* (Linnaeus).—This is an uncommon summer resident in marshland. Nesting records or specimens taken in the breeding season come from Finney, Barton, Jefferson, Douglas, and Miami counties. First dates of observation in spring are from April 11 to May 9 (the median is May 1); dates when last observed in autumn are from September 30 to November 9 (the median is October 18).

Breeding schedule.—The one dated record comes from August.

Number of eggs.—Clutch-size is around 10 eggs (Davie, 1898).

Nests are on the ground in grassy or herbaceous cover.

Black Rail: *Laterallus jamaicensis jamaicensis* (Gmelin).—This is an uncommon summer resident in Kansas. Records of breeding and specimens taken in the breeding season come from Finney, Meade, Riley, and Franklin counties. Seasonal occurrence is within the period March 18 to September 26.

Breeding schedule.—Eggs are laid at least in June.

Number of eggs.—Clutch-size is about 8 eggs (6-10; 4).

Nests are on the ground under cover of marsh plants.

Common Gallinule: *Gallinula chloropus cachinnans* Bangs.—This is a local summer resident in marshlands. Nesting records and specimens taken in the breeding season come from Barton, Stafford, Shawnee, Douglas, and Coffey counties. Occurrence in the State is from April through September.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is about 10 eggs.

Nests are in marsh grasses and other emergent vegetation, not necessarily over water.

American Coot: *Fulica americana americana* Gmelin.—This is an uncommon, local summer resident in wetlands in Kansas. Coots are at greatest abundance in autumnal and spring migratory movements, but are present all year. Nesting has been recorded from Barton, Stafford, Doniphan, and Douglas counties.

Breeding schedule.—Thirty-eight records of breeding span the period May 11 to June 30; the mode to laying is May 25. Earlier breeding probably occurs in the State.

Number of eggs.—Clutch-size is 8 eggs (7.7, 5-12; 28).

Nests are made of marsh vegetation (arrowhead, cattail) and float on water.

Snowy Plover: *Charadrius alexandrinus tenuirostris* (Lawrence).—This summer resident is fairly common on the saline flats of central and south-central Kansas. Breeding records are from Barton, Stafford, Meade, Clark, and Comanche counties.

Breeding schedule.—Fifteen records show that eggs are laid in the period May 25 to June 20; the peak of laying seems to be around June 10.

Number of eggs.—Clutch-size is 3 eggs.

Eggs are deposited on bare sand.

Killdeer: *Charadrius vociferus vociferus* Linnaeus.—This summer resident is common throughout the State, in open country frequently near wetlands. A few individuals overwinter in Kansas, especially in the southern counties.

Breeding schedule.—The 29 records of breeding span the period March 21 to June 30; the modal date of laying is May 20. The distribution of completed clutches (Fig. 3) suggests that Killdeers are here double-brooded.

Number of eggs.—Clutch-size is 4 eggs.

Eggs are laid on the surface of the ground, frequently on gravel, field stubble, plowed earth, and pasture.

Mountain Plover: *Eupoda montana* (Townsend).—This is an uncommon and local summer resident in western short-grass prairie. Breeding records come from Greeley and Decatur counties.

Breeding schedule.—Wolfe (1961) wrote that the species in Decatur County laid eggs in the "last of May" in the early 1900s. The only other dated breeding record is of downy young (KU 5512, 5513) taken on June 21.

Number of eggs.—Clutch-size is usually 3 eggs.

Eggs are laid in slight depressions in the ground, "lined with a few grass stems," according to Wolfe (1961).

American Woodcock: *Philohela minor* (Gmelin).—This is a rare summer

resident in wet woodlands in eastern Kansas. Arrival in the northeast is from mid-March through April, with departures southward occurring from September to December; the last date on which the species has been seen in any year is December 5. There are nesting records only from Woodson County; probably the species nests in Douglas County (Fitch, 1958:194).

Breeding schedule.—Eggs are laid in April.

Number of eggs.—Clutch-size is usually 4 eggs.

Nests are depressions in the dry ground within swampy places, usually under heavy plant cover.

Long-billed Curlew: *Numenius americanus americanus* Bechstein.—This is an uncommon summer resident in western Kansas, in prairie grassland. Breeding records are from Stanton and Morton counties.

Breeding schedule.—Eggs are laid at least in May and June.

Number of eggs.—Clutch-size is 4 eggs.

Eggs are laid in slight depressions in the ground in grassy cover.

Upland Plover: *Bartramia longicauda* (Bechstein).—This is a locally common summer resident, most conspicuously in the Flint Hills, in grassland. Breeding records are from Trego, Hamilton, Finney, Morton, Meade, Marion, Chase, Kearny, Butler, Cowley, Douglas, Johnson, Wabaunsee, Franklin, Anderson, and Coffey counties. Dates of first arrival in spring span the period April 2 to May 5 (the median is April 19), and dates last seen in autumn are from September 3 to October 6 (the median is September 13).

Breeding schedule.—Sixteen records of breeding span the period April 21 to June 10; the modal date for egg-laying is May 5.

Number of eggs.—Usually 4 eggs are laid.

Eggs are placed on vegetation on the ground surface, in pasture, field stubble, or gravel, frequently under heavy plant cover.

Spotted Sandpiper: *Actitis macularia* (Linnaeus).—This summer resident is locally common on wet ground and along streams. Dates of arrival in spring are from March 29 to April 30 (the median is April 24), and dates of last observation in autumn span the period September 2 to October 10 (the median is September 18).

Breeding schedule.—Egg records are all from the northeastern sector, and all are for May.

Number of eggs.—Usually 4 eggs are laid.

Nests are of plant fibers in depressions in dry ground on gravel banks, pond or stream borders, or in pastureland.

American Avocet: *Recurvirostra americana* Gmelin.—This is a local summer resident in marshes in central and western Kansas. There are breeding records from Finney, Barton, and Stafford counties. Extreme dates within which avocets have been recorded are April 2 to November 21.

Breeding schedule.—Forty-one records of breeding span the period May 11 to June 20 (26 records shown in Fig. 3); the modal date for laying is June 5.

Number of eggs.—Usually 4 eggs are laid.

Nests are placed on the surface of the ground, near water.

Wilson Phalarope: *Steganopus tricolor* Vieillot.—This is a local summer resident in marshes in central and western Kansas, but breeding records are

available only from Barton County. The earliest date of occurrence is April 7 and the latest is October 14.

Breeding schedule.—Ten records indicate eggs are laid in May and June.

Number of eggs.—Three or 4 eggs are laid.

Nests are of plant stems in slight depressions in the ground.

Forster Tern: *Sterna forsteri* Nuttall.—This is a local summer resident in central Kansas, in marshes. There are breeding records only from Cheyenne Bottoms, Barton County (Zuvanich, 1963:1). First dates of arrival in spring span the period April 9 to 29 (the median is April 22), and apparent departure south in autumn occurs from August 1 to November 1 (the median is September 3).

Breeding schedule.—Twenty-three records of nesting are from late May to mid-June; all records are for the year 1962.

Number of eggs.—Usually 4 eggs are laid.

Nests are frequently floating platforms of vegetation (algae, cattail, and the like) in shallow water; old nests of Pied-billed Grebes are sometimes used as bases, and occasionally the birds nest on the ground.

Least Tern: *Sterna albifrons athalassos* Burleigh and Lowery.—This tern is a local summer resident in marshes and along streams in central and western Kansas. There are breeding records from Hamilton, Meade, and Stafford counties. First dates of arrival in spring are from May 14 to 30 (the median is May 28), and last dates of occurrence in autumn are from August 9 to September 7 (the median is August 25).

Breeding schedule.—Twenty-one records of egg-laying are from May 21 to June 30 (Fig. 4); the modal date for laying is June 5.

Number of eggs.—Two, 3 or 4 eggs are laid.

Eggs are laid on the bare ground, usually a sandy surface, near water.

Black Tern: *Chlidonias niger surinamensis* (Gmelin).—This is a local summer resident in marshlands in central Kansas. There are breeding records only from Barton County for 1961 and 1962; possibly the species breeds in Douglas County. First dates of arrival in spring are from May 3 to 29 (the median is May 14), and last dates of occurrence in autumn are from September 2 to 30 (the median is September 11).

Breeding schedule.—Twenty-four sets of eggs (Parmelee, 1961:25; M. Schwilling) were complete between June 11 and July 12.

Number of eggs.—Clutch-size is 3 eggs.

Nests are of dead plant matter placed on floating parts of emergent green plants in shallow water.

Rock Dove: *Columba livia* Gmelin.—This species was introduced into North America by man from European stocks of semi-domesticated ancestry. "Pigeons" now are feral around towns and farms, and cliffsides in the west, and are locally common permanent residents throughout the State.

Breeding schedule.—Eggs are laid in every month of the year. The main season of breeding is spring, and this is depicted in Figure 4; the 26 records of breeding by feral birds are from January 11 to June 10, and the modal date of laying is probably April 5.

Number of eggs.—Pigeons usually lay 2 eggs.

Nests are of sticks and other plant matter placed on ledges and recesses of buildings, bridges, and cliffs, 10 to 60 feet high.

Mourning Dove: *Zenaidura macroura marginella* (Woodhouse).—This is a common summer resident throughout the State, in open country and woodland edge. The species is also present in winter in much reduced numbers, and many are transient in periods of migration. The time of greatest abundance is from March to November. Doves of extreme eastern Kansas have by some workers been referred to the subspecies Z. *m. carolinensis* (Linnaeus); specimens at the Museum of Natural History indicate that these doves are

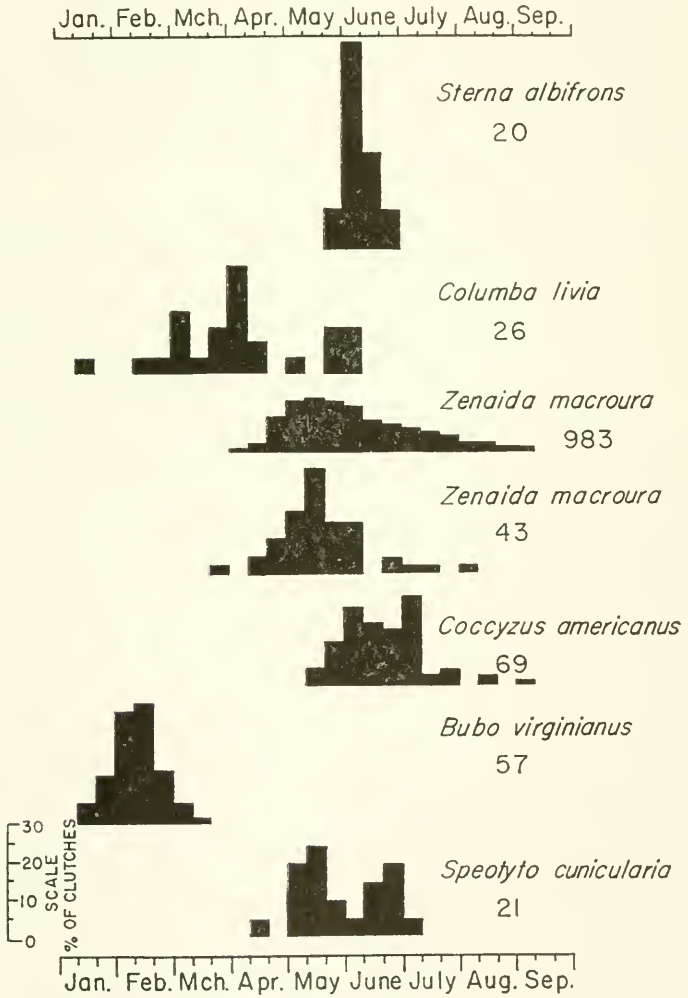

FIG. 4.—Histograms representing breeding schedules of the Least Tern, two doves, the Yellow-billed Cuckoo, and two owls in Kansas. See legend to Figure 1 for explanation of histograms.

best regarded as members of populations of intermediate subspecific, or morphologic, affinities, and that they are satisfactorily included within *Z. m. marginella.*

Breeding schedule.—Numerous (983) records of egg-laying from north-central Kansas are from April 1 to September 10; the modal date for laying is May 15. Forty-three records of breeding from northeastern Kansas span the period March 21 to August 10; the modal date of laying is May 15. These samples are depicted in Figure 4.

Both sets of data are shown here to illustrate some of the differences between large and small samples of heterogeneous data. The small sample tends to be incomplete both early and late in the season, and the mode tends to be conspicuous. Yet, the modes for the two samples coincide. Also, the data from the north-central sector indicate that egg-laying in March would be found less than once in 983 records, but the small sample from the northeast includes one record for March. Such an instance doubtless reflects, at least in part, the fact that the two geographic sectors have different environmental conditions, but it is likely that the instance also partly reflects the unpredictable nature of sampling.

Number of eggs.—Doves lay two eggs. About one per cent of all nests have 3 eggs, but it is not known for any of these whether one or two females were responsible.

Nests are placed in a wide variety of plants, or on the ground. The commonest plants are those used most frequently; in north-central Kansas one-third of all nests are placed in osage orange trees, but in the northeast elms are most frequently used. Nestsites are from zero to 15 feet high.

Yellow-billed Cuckoo: *Coccyzus americanus americanus* (Linnaeus).—This is a common summer resident in riparian and second-growth habitats throughout the State. Twenty-three dates of first arrival in spring fall between April 29 and May 22 (the median is May 12), and nine dates of last observation in autumn run from September 13 to October 12 (the median is September 23).

Breeding schedule.—Sixty-nine records of egg-laying span the period May 11 to September 10 (Fig. 4); the modal date of laying is June 5.

Number of eggs.—Clutch-size is 3 eggs (3.1, 2-5; 54).

Nests are placed about six feet high (from four to 20 feet) in sumac, rose, pawpaw, mulberry, elm, cottonwood, willow, redbud, oak, osage orange, walnut, boxelder, usually on horizontal surfaces, and in heavy cover.

Black-billed Cuckoo: *Coccyzus erythropthalmus* (Wilson).—This is an uncommon summer resident, occurring in heavy riparian shrubbery and second-growth. Breeding records are chiefly from eastern Kansas, but specimens have been taken in the breeding season in all parts of the State. Eleven dates of first arrival in spring are from May 7 to May 30 (the median is May 19), and four dates of last observed occurrence in autumn are between September 4 and October 7 (the average is September 18).

Breeding schedule.—Seventeen records of egg-laying are between May 21 and August 10; the mode is at June 5.

Number of eggs.—Clutch-size is 2 to 3 eggs (2.5, 2-3; 13).

Nests are placed about four feet high in heavy cover in plum, elm, locust, and the like.

Roadrunner: *Geococcyx californianus* (Lesson).—This is a local resident in southern Kansas in xeric scrub or open edge habitats. Breeding records are from Cowley and Sumner counties.

Breeding schedule.—Eggs are laid at least from early April to mid-July.

Number of eggs.—Clutch-size is about 5 eggs (4.5, 3-6; 4).

Nests are placed on the ground under plant cover, or occasionally low in bushes.

Barn Owl: *Tyto alba pratincola* Bonaparte.—This resident has a low density throughout Kansas in open woodland and near agricultural enterprises of man.

Breeding schedule.—The few records available indicate egg-laying occurs at least from April to July; elsewhere the species is known to have a more protracted breeding schedule.

Number of eggs.—Clutch-size is about 5 eggs (4.7, 2-6; 4).

Nests are informal aggregations of sticks and litter placed in recesses in stumps, hollow trees, rocky and earthen banks, and dwellings and outbuildings of man.

Screech Owl: *Otus asio* (Linnaeus).—This is a common resident in woodland habitats throughout Kansas. *O. a. aikeni* (Brewster) occurs west of Rawlins, Gove, and Comanche counties, and *O. a. naevius* (Gmelin) occurs in the remainder of the State except for the eastern south-central sector, occupied by *O. a. hasbroucki* Ridgway.

Breeding schedule.—Fifteen records of egg-laying span the period March 20 to May 10; there is a strong mode at April 5.

Number of eggs.—Clutch-size is 4 eggs (4.0, 3-6; 12).

Nests are placed in holes and recesses in trees, three to 20 feet high.

Great Horned Owl: *Bubo virginianus* (Gmelin).—This is a common resident throughout Kansas, especially near woodlands and cliffsides. *B. v. virginianus* (Gmelin) occurs east of a line through Rawlins and Meade counties and *B. v. occidentalis* Stone occurs to the west.

Breeding schedule.—Fifty-seven records of egg-laying span the period January 11 to March 20 (Fig. 4); the modal date for laying is near February 10.

Number of eggs.—Clutch-size is 2 eggs (2.4, 2-3; 22).

Nests are placed about 30 feet high in cottonwood, elm, osage orange, hackberry, juniper, locust, cliffsides, and buildings of man. Old nests of hawks, crows, and herons are frequently appropriated.

Burrowing Owl: *Speotyto cunicularia hypugaea* (Bonaparte).—This is an uncommon summer resident in western Kansas in grassland and open scrub habitats. Stations of breeding all come from west of a line running through Cloud and Barber counties. Arrival in spring is between March 22 and April 17 (the median for 7 records is April 9), and dates last seen in autumn span the period September 8 to November 14 (the median for 9 records is September 26).

Breeding schedule.—Twenty-one records of egg-laying run from April 11 to July 10 (Fig. 4); the mode of laying is May 15.

Number of eggs.—Clutch-size is 7 or 8 eggs.

Nests are informal aggregations of plant and animal fibers in chambers of earthen burrows usually made by badgers or prairie dogs.

Barred Owl: *Strix varia varia* Barton.—This is a local resident in eastern Kansas, in heavy woodland. The species is said by implication (A. O. U. Check-list, 1957) to occur in western Kansas, but no good breeding records are available, all such records coming from and east of Morris County. Specimens from southeastern Kansas show morphologic intergradation with characters of *S. v. georgica* Latham.

Breeding schedule.—Three records of egg-laying are for the first half of March.

Number of eggs.—Clutch-size in our sample is 2 eggs.

Nests are situated in cavities in trees or in old hawk or crow nests.

Long-eared Owl: *Asio otus wilsonianus* (Lesson).—This owl is a local resident or summer resident in woodland with heavy cover throughout the State. Breeding records are available from Trego, Meade, Cloud, and Douglas counties.

Breeding schedule.—Four records of egg-laying are for the period March 11 to April 10.

Number of eggs.—Clutch-size is 5 or 6 eggs.

Nests are placed in hollows of trees, stumps, cliffsides, on the ground surface, or in old hawk, crow, or magpie nests (Davie, 1898).

Short-eared Owl: *Asio flammeus flammeus* (Pontoppidan).—This is a local resident or summer resident in open, marshy, and edge habitats; records of nesting come from Republic, Marshall, Woodson, and Bourbon counties.

Breeding schedule.—Eggs are laid at least in April.

Number of eggs.—Clutch-size is about 6 eggs (Davie, 1898).

Nests are simple structures of sticks and grasses, placed on the ground in grasses, frequently near cover of downed timber or bushes.

Saw-whet Owl: *Aegolius acadicus acadicus* (Gmelin).—This is a rare and local resident, in woodland. There is one breeding record (summer, 1951, Wyandotte County; Tordoff, 1956:331).

Chuck-will's-widow: *Caprimulgus carolinensis* Gmelin.—This is a locally common summer resident in woodland habitats in eastern Kansas. Stations of occurrence of actual breeding fall south of Wyandotte County and east of Shawnee, Greenwood, Stafford, and Sedgwick counties.

Breeding schedule.—Five records of breeding come between April 21 and May 31, with a peak perhaps in the first third of May.

Number of eggs.—Clutch-size is 2 eggs.

Eggs are laid on heavy leaf-litter, usually under shrubby cover.

Whip-poor-will: *Caprimulgus vociferus vociferus* Wilson.—This is a local summer resident in woodland in eastern Kansas. Breeding records are available only from Doniphan, Leavenworth, and Douglas counties; there are sight records in summer from Shawnee County.

Breeding schedule.—Two records of breeding cover the period May 21 to June 20.

Number of eggs.—Clutch-size is 2 eggs.

Eggs are laid on heavy leaf-litter in shrubby cover.

Poor-will: *Phalaenoptilus nuttallii nuttallii* (Audubon).—This is a common summer resident in western Kansas, in xeric, scrubby woodland. Breeding

TABLE 12.—OCCURRENCE IN TIME OF SUMMER RESIDENT CAPRIMULGIDS AND APODIDS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Chuck-will's-widow	Apr. 20–May 1	Apr. 28	Oct.–Dec.	Oct.?
Whip-poor-will	Apr. 6–Apr. 25	Apr. 17	Sept. 10–Oct. 11	Sept. 21
Poor-will	Apr. 12	.....	Sept. 20	.....
Common Nighthawk	Apr. 29–May 23	May 15	Sept. 13–Oct. 18	Sept. 23
Chimney Swift	Apr. 2–Apr. 30	Apr. 22	Sept. 18–Oct. 30	Oct. 4
Ruby-throated Hummingbird	Apr. 2–May 19	May 6	Sept. 3–Oct. 15	Sept. 10

records are chiefly from west of Riley County, but there is one from Franklin County; specimens taken in the breeding season are available from Doniphan, Douglas, Anderson, Woodson, and Greenwood counties.

Breeding schedule.—Six records of egg-laying are from the period May 1 to June 20.

Number of eggs.—Clutch-size is 2 eggs.

Eggs are laid on the ground, with or without plant cover.

Common Nighthawk: *Chordeiles minor* (Forster).—This is a common summer resident throughout Kansas. Temporal occurrence is indicated in Table 11. Three subspecies reach their distributional limits in the State, *C. m. minor* (Forster) in northeastern Kansas, *C. m. chapmani* Coues in southeastern Kansas, and *C. m. howelli Oberholser* west of the Flint Hills.

Breeding schedule.—Twenty-two records of breeding span the period May 11 to June 30; the modal date for egg-laying is June 10 (Fig. 5).

Number of eggs.—Clutch-size is 2 eggs.

Eggs are laid on the ground in rocky or gravelly areas, on unpaved roads, or on flat, gravelled tops of buildings of man.

Chimney Swift: *Chaetura pelagica* (Linnaeus).—This is a common summer resident in eastern Kansas, around towns. Temporal occurrence in the State is indicated in Table 12.

Breeding schedule.—Thirty-six records of breeding span the period May 11 to June 30; the modal date for egg-laying is May 25 (Fig. 5).

Number of eggs.—Clutch-size is about 4 eggs.

Nests are secured by means of a salivary cement to vertical surfaces, usually near the inside tops of chimneys in dwellings of man, but occasionally in abandoned buildings and hollow trees.

Ruby-throated Hummingbird: *Archilochus colubris* (Linnaeus).—This is an uncommon summer resident in eastern Kansas, and is rare in the west, in towns and along riparian vegetation. Temporal occurrence in the State is listed in Table 12.

Breeding schedule.—Eight records of breeding fall within the period May 21 to July 10; there seems to be a peak to laying in the last third of June.

Number of eggs.—Clutch-size is 2 eggs.

Most nests are on outer branches of shrubs and trees, in forks or on pendant branches, 10 to 20 feet high.

Belted Kingfisher: *Megaceryle alcyon alcyon* (Linnaeus).—This summer resident is common throughout the State in streamside and lakeside habitats. Timing of arrival and departure of the breeding birds is not well-documented owing to the fact that the species is also transient and a winter resident in the State.

Breeding schedule.—Eggs are laid at least from April 21 to May 20.

Number of eggs.—Clutch-size is near 6 eggs.

Eggs are laid on the floor of the chamber at the inner end of a horizontal tunnel excavated in an earthen bank. The tunnel is two to six feet long and many tunnels are strewn with bones and other dietary refuse.

Yellow-shafted Flicker: *Colaptes auratus* (Linnaeus).—This is a common resident and summer resident in eastern Kansas, meeting, hybridizing with, and partly replaced by *Colaptes cafer* westward, in open woodlands. *C. a. auratus* (Linnaeus) occurs in southeastern Kansas, and *C. a. luteus* Bangs occurs in the remainder, intergrading west of the Flint Hills with *C. cafer.*

Breeding season.—Forty-eight records of breeding span the period April 11 to June 10; the modal date for egg-laying is May 10 (Fig. 5). This sample is drawn from central and eastern Kansas, but includes records of breeding by some birds identified in the field as *C. cafer.*

Number of eggs.—Clutch-size is about 6 eggs.

Nests are piles of wood chips in cavities excavated in stumps and dead limbs of trees such as willow, cottonwood, mulberry, and catalpa, ordinarily about six feet above the ground.

Red-shafted Flicker: *Colaptes cafer collaris* Vigors.—This woodpecker is a common summer resident in western Kansas, meeting, hybridizing with, and largely replaced by *C. auratus* in central and eastern sectors. The vast majority of specimens taken in Kansas show evidence of intergradation with *C. auratus.*

Breeding schedule.—The few records of flickers identified in the field as *C. cafer* have been combined with those of *C. auratus* (Fig. 5).

Number of eggs.—Clutch-size is perhaps 6 eggs.

Nests are like those of *C. auratus.*

Pileated Woodpecker: *Dryocopus pileatus* (Linnaeus).—This is a rare and local resident in the east, in heavy timber. The species has been seen, chiefly in winter, in all sectors of eastern Kansas in recent years, but actual records of breeding come only from Linn and Cherokee counties. *D. p. abieticola* (Bangs) occurs in the northeast, and *D. p. pileatus* (Linnaeus) in the southeast.

Breeding schedule.—Eggs are laid at least in April.

Number of eggs.—Clutch-size is 3 or 4 eggs.

Nests are of wood chips in cavities excavated 45 to 60 feet high in main trunks of cottonwood, sycamore, and pin oak.

Red-bellied Woodpecker: *Centurus carolinus zebra* (Boddaert).—In woodland habitats this is a common resident in eastern Kansas, local in the west.

Breeding schedule.—Thirty-seven records of breeding span the period March 1 to June 30 (Fig. 5); the modal date of egg-laying is around April 25.

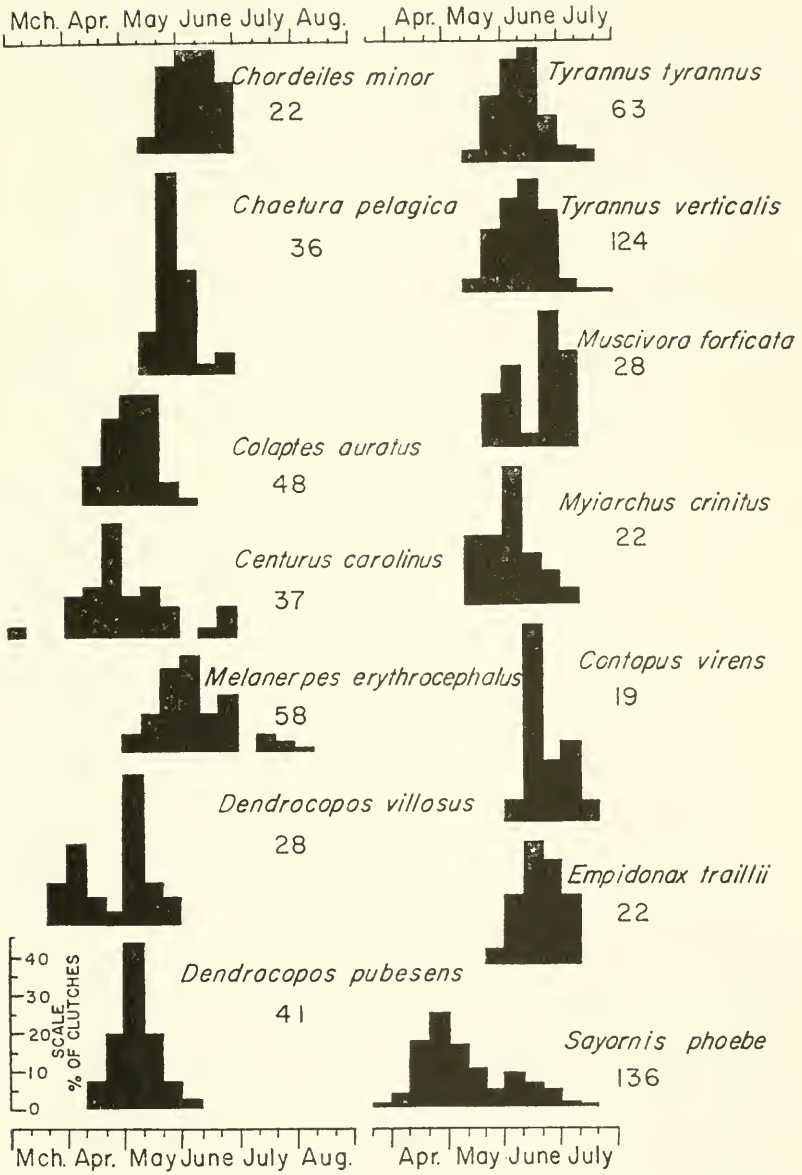

FIG. 5.—Histograms representing breeding schedules of the Common Nighthawk, Chimney Swift, woodpeckers, and flycatchers in Kansas. See legend to Figure 1 for explanation of histograms.

Number of eggs.—Clutch-size is about 5 eggs.

Nests are of wood chips in cavities excavated in elm, cottonwood, box elder, ash, hickory, or willow, about 25 feet high (nine to 60 feet).

Red-headed Woodpecker: *Melanerpes erythrocephalus* (Linnaeus).—This is a common summer resident and uncommon permanent resident in open woodland; in winter it is noted especially around groves of oaks. *M. e. erythrocephalus* (Linnaeus) occurs in eastern Kansas and *M. e. caurinus* Brodkorb occurs in central and western Kansas.

Breeding schedule.—Fifty-eight records of breeding span the period May 1 to August 10 (Fig. 5); the modal date of egg-laying is June 5.

Number of eggs.—Clutch-size is 3 or 4 eggs.

Nests are of wood chips in cavities excavated about 25 feet high in willow, cottonwood, and elm.

Hairy Woodpecker: *Dendrocopos villosus villosus* (Linnaeus).—This resident is common in woodlands throughout the State.

Breeding schedule.—Twenty-eight records of breeding span the period March 21 to May 30 (Fig. 5); the modal date of egg-laying is May 5.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are of wood chips in cavities excavated about 13 feet high in elm, honey locust, and ash.

Downy Woodpecker: *Dendrocopos pubescens* (Linnaeus).—This resident is common in woodland throughout the State. *D. p. pubescens* (Linnaeus) occurs in southeastern Kansas, and *D. p. medianus* (Swainson) in the remainder.

Breeding schedule.—Forty-one records of breeding span the period April 11 to June 10 (Fig. 5); the modal date of egg-laying is May 5.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are of wood chips in cavities excavated about 20 feet high in willow, honey locust, ash, apple, and pear.

Eastern Kingbird: *Tyrannus tyrannus* (Linnaeus).—This summer resident is common throughout the east; it is local in the west but there maintains conspicuous numbers in favorable places, such as riparian woodland; preferred habitat in eastern sectors is typically in woodland edge. Temporal occurrence is indicated in Table 13.

Breeding season.—Sixty-three dates of egg-laying span the period May 11 to July 20 (Fig. 5); the modal date for completion of clutches is June 15. Nearly 70 per cent of all eggs are laid in June.

Number of eggs.—Clutch-size is 3 eggs (3.3, 2-3; 10). Clutches are probably larger than the average in May and smaller in June and July.

Nests are placed in crotches, terminal forks, and some on tops of limbs, about 16 feet high, in elm, sycamore, honey locust, willow, oak, apple, and red cedar.

Western Kingbird: *Tyrannus verticalis* Say.—This summer resident is common in the west, but is local and less abundant in the east. Preferred habitat is in woodland edge, open country with scattered trees, and in towns. Temporal occurrence is indicated in Table 13.

Breeding schedule.—The 124 dates of egg-laying span the period May 11 to July 31 (Fig. 5); the modal date for egg-laying is June 15. More than 70 per cent of all clutches are laid in June.

Number of eggs.—Clutch-size is 4 eggs (3.6, 3-4; 8).

Nests are placed in crotches, lateral forks, or on horizontal limbs, about 26 feet high, in cottonwood, elm, osage orange, hackberry, honey locust, mulberry, oak, and on power poles.

Scissor-tailed Flycatcher: *Muscivora forficata* (Gmelin).—This summer resident is common in central and southern Kansas; it is rare to absent in the northwestern sector, and is local in the northeast. Preferred habitat is in open country with scattered trees. Temporal occurrence is indicated in Table 13.

Breeding schedule.—Twenty-eight records of breeding occur from May 21 to July 10 (Fig. 5); the modal date of egg-laying is June 25. The present sample of records is small, and there is otherwise no evidence suggesting that the breeding schedule of this species differs from those of the other two kingbirds in Kansas.

Number of eggs.—Clutch-size is 3 eggs (3.2, 2-5; 17). Mean clutch-size for the first peak of laying shown in Figure 5 is 4.0 eggs; that for the second peak is 2.7 eggs.

Nests are placed in forks or on horizontal limbs of osage orange, red haw, elm, and on crosspieces of power poles, about 15 feet high (ranging from five to 35 feet).

Great Crested Flycatcher: *Myiarchus crinitus boreus* Bangs.—This summer resident is common in eastern Kansas, but is less numerous in the west. Preferred habitat is in woodland and woodland edge. Temporal occurrence is indicated in Table 13.

Breeding schedule.—The twenty-two records of egg-laying are in the period May 11 to July 10 (Fig. 5); the modal date for egg-laying is June 5. The shape of the histogram (Fig. 5) indicates that some breeding for which records are lacking occurs earlier in May.

TABLE 13.—OCCURRENCE IN TIME OF SUMMER RESIDENT FLYCATCHERS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Eastern Kingbird	Apr. 22–Apr. 30	Apr. 28	Sept. 1–Sept. 24	Sept. 13
Western Kingbird	Apr. 23–Apr. 30	Apr. 28	Sept. 1–Sept. 26	Sept. 8
Scissor-tailed Flycatcher	Apr. 15–Apr. 28	Apr. 18	Sept. 21–Oct. 22	Oct. 12
Great Crested Flycatcher	Apr. 15–May 4	Apr. 29	Sept. 1–Sept. 21	Sept. 9
Eastern Phoebe	Mar. 3–Mar. 31	Mar. 22	Oct. 3–Oct. 27	Oct. 9
Say Phoebe	Apr. 4–Apr. 22	Apr. 12	.....	.....
Acadian Flycatcher	Apr. 30–May 19	May 9	Sept. 3–Sept. 17	Sept. 4
Eastern Wood Pewee	Apr. 2–May 28	May 19	Aug. 30–Sept. 18	Sept. 6

Number of eggs.—Clutch-size is 5 eggs (4.8, 4-6; 6).

Nests are placed in hollows and crevices in elm, maple, cottonwood, willow, pear, apple, oak, drain spouts, and, occasionally, "bird houses" made by man, about 17 feet high (four to 45 feet high).

Eastern Phoebe: *Sayornis phoebe* (Latham).—This summer resident is common in eastern Kansas, but is local in the west. Preferred habitat is in woodland edge and riparian groves, where most birds are found near bridges, culverts, or isolated outbuildings of man. Temporal occurrence is indicated in Table 13.

Breeding schedule.—The 136 records of breeding span the period March 21 to July 20 (Fig. 5); the modal date for egg-laying is April 25 (for first clutches) and June 5 (for second clutches); this species seems to be the only double-brooded flycatcher in Kansas.

Number of eggs.—Clutch-size is 4 to 5 eggs (4.2, 3-5; 58). The seasonal progression in clutch-size can be summarized as follows:

March 21-April 10: 4.0 eggs (2 records)
April 11-May 10: 4.4 eggs (37 records)
May 11-June 10: 3.9 eggs (10 records)
June 11-July 20: 3.6 eggs (9 records)

Nests are placed on horizontal, vertical, or overhanging surfaces of culverts, bridges, houses of man, earthen cliffs, rocky ledges, and entrances to caves, at an average height of 7.8 feet.

Say Phoebe: *Sayornis saya saya* (Bonaparte).—This is a common summer resident in western Kansas, breeding at least east to Cloud County, in open country. Occurrence in time is listed in Table 13.

Breeding schedule.—Ten records of breeding fall in the period May 1 to July 20; the modal date for egg-laying is in late May.

Number of eggs.—Clutch-size is about 5 eggs.

Nests are placed under bridges, in houses, or on cliffsides and earthen banks.

Acadian Flycatcher: *Empidonax virescens* (Vieillot).—This is an uncommon summer resident in eastern Kansas, in woodland and riparian habitats. Temporal occurrence is indicated in Table 13.

Breeding schedule.—The available records of breeding by this species in Kansas are too few to indicate reliably the span of the breeding season. Information on hand suggests that Acadian Flycatchers lay most eggs in late May or early June, and this places their nesting peak some 10 to 20 days earlier than peaks for Wood Pewees and Traill Flycatchers.

Number of eggs.—Five records show 3 eggs each.

Nests are placed about six feet high on terminal twigs of oak and alder.

Traill Flycatcher: *Empidonax traillii traillii* (Audubon).—This flycatcher has only recently been found nesting within Kansas; the species is not included in analyses above. Twenty-three nesting records are here reported, for the species in Kansas City, Jackson and Platte counties, Missouri. Most of these records are from within a few hundred yards of the political boundary of Kansas. The Traill Flycatcher is a local summer resident in extreme northeastern Kansas (Doniphan County), in wet woodland and riparian groves.

Temporal occurrence is not well-documented; first dates run from May 19 to 25; the last dates of annual occurrence, possibly not all for transients, run from August 14 to September 24.

Breeding schedule.—Twenty-three records of breeding are from May 21 to July 10 (Fig. 5); the modal date for egg-laying is June 15.

Number of eggs.—Clutch-size is 3 eggs (3.4, 2-5; 22).

Nests are placed in forks, crotches, and occasionally near trunks, chiefly of willow, from 4.5 to 12 feet high (averaging six feet).

Eastern Wood Pewee: *Contopus virens* (Linnaeus).—This summer resident is common in the east, but is rare in the west. Preferred habitat is in edge of forest and woodland. Temporal occurrence is indicated in Table 13.

Breeding schedule.—Nineteen dates of egg-laying span the period June 1 to July 20 (Fig. 5); the modal date for completion of clutches is June 15, and more than half of all clutches are laid in the period June 11 to 20.

Number of eggs.—Clutch-size is about 3 eggs.

Nests are placed on upper surfaces of horizontal limbs of oak, elm, and sycamore, about 22 feet high.

Horned Lark: *Eremophila alpestris* (Linnaeus).—Breeding populations are resident in open country with short or cropped vegetation. *E. a. praticola* (Henshaw) lives in the east, and *E. a. enthymia* (Oberholser) in the west.

Breeding schedule.—Twenty-one records of breeding span the period March 11 to June 10 (Fig. 6); the modal date for egg-laying is March 25. The histogram (Fig. 6) is constructed on a clearly inadequate sample, and records of breeding both earlier and later are to be expected. The peak of first nesting activity is probably reasonably well-indicated by the available records.

Number of eggs.—Clutch-size is 3 eggs (3.6, 3-5; 16).

Nests are placed on the ground, usually amid short vegetation such as cropped prairie grassland or cultivated fields (notably soybeans and wheat), and occasionally on bare ground.

Tree Swallow: *Iridoprocne bicolor* (Vieillot).—This is a summer resident in extreme northeastern Kansas; nesting birds have been found only along the Missouri River in Doniphan County. Habitat is in open woodland, and in Kansas is always associated with water. Temporal occurrence in the State is indicated in Table 14.

TABLE 14.—OCCURRENCE IN TIME OF SUMMER RESIDENT SWALLOWS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Tree Swallow	Apr. 5–Apr. 30	Apr. 24	Sept. 30–Oct. 21	Oct. 8
Bank Swallow	Apr. 9–May 19	May 7	Sept. 3–Sept. 20	Sept. 10
Rough-winged Swallow	Mar. 29–May 30	Apr. 22	Sept. 23–Oct. 21	Oct. 10
Cliff Swallow	Apr. 14–May 27	May 11	Sept. 3–Oct. 25	Sept. 11
Barn Swallow	Mar. 31–Apr. 29	Apr. 21	Sept. 22–Oct. 25	Oct. 7
Purple Martin	Mar. 5–Apr. 9	Mar. 26	Aug. 28–Sept. 23	Sept. 3

Breeding schedule.—Eight records of breeding span the period May 21 to June 20; the modal date for egg-laying is May 25. The small sample may not accurately reflect the peak of nesting activity.

Number of eggs.—Clutch-size is 5 or 6 eggs (5.5, 5-6; 4).

Nests are placed chiefly in abandoned woodpecker diggings in willows, four to ten feet high, over water.

Bank Swallow: *Riparia riparia riparia* (Linnaeus).—This summer resident is common wherever cut-banks suitable for nesting activities allow relatively undisturbed behavior. The species is almost always found near water. Temporal occurrence is indicated in Table 14.

Breeding schedule.—Sixty records of breeding span the period May 11 to June 20 (Fig. 6); the modal date for completion of clutches is June 5.

Nearly 75 per cent of all clutches are laid in the period May 21 to June 10. Under unusual circumstances time of breeding can be greatly delayed; such circumstances occurred in 1961 in many places along the Kansas River in eastern Kansas, where the soft, sandy-clay banks were repeatedly washed away in May and June by high water undercutting the cliffs. Bank Swallows attempted to work on burrows in late May, but stabilization of the banks occurred only by late June, and the peak of egg-laying for many colonies was around July 12. Records for 1961 are omitted from the sample used here (Fig. 6).

Number of eggs.—Clutch-size is 5 eggs (4.8, 3-7; 60). Yearly clutch-size at one colony 3 miles east of Lawrence, Douglas County, is as follows:

1959: 5.2, 19 records	1961: 3.7, 11 records
1960: 5.0, 12 records	1962: 4.8, 18 records

The sample for 1961 is that taken in early July when breeding occurred after a delay of more than a month, as described above.

Nesting chambers are excavated in sandy-clay banks, piles of sand, piles of sawdust, or similar sites, at ends of tunnels one to more than three feet in depth from the vertical face of the substrate.

Rough-winged Swallow: *Stelgidopteryx ruficollis serripennis* (Audubon).—This summer resident is common in most places; it is not restricted to a single habitat, but needs some sort of earthen or other substrate with ready-made burrows for nesting. Temporal occurrence is indicated in Table 14.

Breeding schedule.—The 14 records of breeding are in the period May 11 to June 30; the modal date of egg-laying is June 5. Seventy per cent of all eggs are laid in the period May 21 to June 10.

Number of eggs.—Clutch-size is 5 eggs (5.0, 4-6; 4).

Nesting chambers are in old burrows of Bank Swallows, Kingfishers, rodents, or in crevices remaining subsequent to decomposition of roots of plants; frequently this swallow uses a side chamber off the main tunnel, near the mouth, of a burrow abandoned or still in use by the other species mentioned above.

Cliff Swallow: *Petrochelidon pyrrhonota pyrrhonota* (Vieillot).—This common summer resident occurs wherever suitable sites for nests are found. Temporal occurrence is indicated in Table 14.

Breeding schedule.—The 610 records of breeding span the period May 21 to June 30 (Fig. 6); the modal date for egg-laying is June 5, and 85 per cent

of all clutches are laid from May 21 to June 10. Such synchronous breeding activity is probably a function of strong coloniality with attendant "social facilitation" of breeding behavior.

Number of eggs.—Clutch-size is 5 eggs (4.9, 3-7; 7).

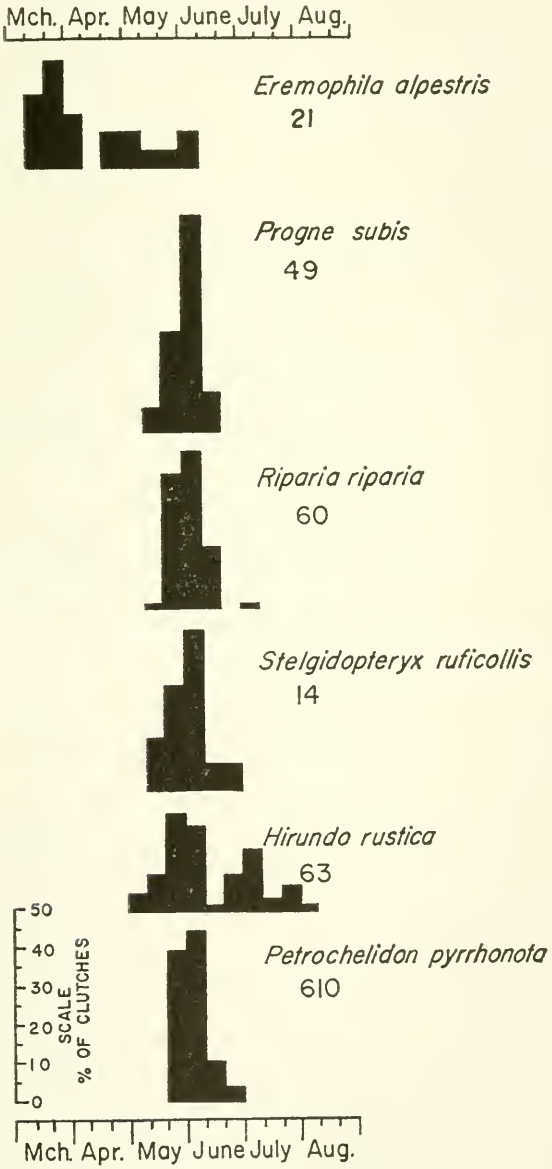

FIG. 6.—Histograms representing breeding schedules of the Horned Lark and swallows in Kansas. See legend to Figure 1 for explanation of histograms.

Nests are built in mud jugs plastered to vertical rock faces, bridges, culverts, and buildings from a few feet to more than 100 feet above the ground.

Barn Swallow: *Hirundo rustica erythrogaster* Boddaert.—This summer resident is common in most habitats, occurring chiefly about cultivated fields and pastures. Temporal occurrence is indicated in Table 14.

Breeding schedule.—Sixty-three records of breeding in northern Kansas span the period May 1 to July 31 (Fig. 6); the modal date for completion of first clutches is May 25, and that for the second is July 5. The schedule of breeding in southern Kansas (chiefly Cowley County), to judge by 41 records, conforms to the one for northern Kansas: the season spans the period May 1 to August 10, and the modal date for first clutches is May 15. The ten-day lag in peak of first clutches of the northern over the southern sample is about what would be expected on the basis of differential inception of the biological growing season from south to north each spring.

Number of eggs.—Clutch-size does not vary geographically, to judge only from the present samples, and all are included in the listing to follow. The modal size of clutches is 5 eggs (4.7, 3-7; 43); clutches from the period May 1 to 30 show an average of 5.0 eggs, from June 1 to 20 an average of 4.9 eggs, and from June 21 to August 10, 4.4 eggs.

Nests are usually placed on horizontal surfaces in barns, sheds, or other such structures; more rarely they are put on bridges, and less frequently yet on vertical walls of culverts or sheds.

Purple Martin: *Progne subis subis* (Linnaeus).—This summer resident is common in the east but rare in the west. The only documented colony west of the 99th meridian was in Oberlin, Decatur County (Wolfe, 1961), occupied some 50 years ago. Temporal occurrence is indicated in Table 14.

Breeding schedule.—The breeding season spans the period May 11 to June 20 (Fig. 6); the modal date of egg-laying is June 5, and 57 per cent of all clutches are laid in the period June 1 to 10.

Number of eggs.—Clutch-size is 5 eggs (4.2, 3-6; 33). Mean clutch-size is 4.3 eggs in May and 4.2 in June. Adults tend to lay clutches of 5 eggs and first-year birds clutches of 4. Replacement clutches by birds of any age tend to be of 3 eggs.

Nests are built of sticks and mud placed in cavities; in Kansas these are almost always in colony houses erected by man. Use of holes and crevices in old buildings is known to have occurred on the campus of The University of Kansas in the nineteen thirties (W. S. Long, 1936, MS), in Oberlin, Decatur County in 1908-1914 (Wolfe, *loc. cit.*), and presently in Ottawa, Franklin County (Hardy, 1961).

Blue Jay: *Cyanocitta cristata bromia* Oberholser.—This resident is common throughout Kansas in woodland habitats. Most first-year birds move south in winter, but adults tend to be strictly permanent residents. Groups of ten to more than 50 individuals can be seen moving south in October and north in April. All individuals taken from such mobile groups are in first-year feather.

Breeding schedule.—Eighty-three records of breeding span the period April 10 to July 10 (Fig. 7); the modal date of egg-laying is May 15, and about 50 per cent of all clutches are laid in the period May 11-31.

Number of eggs.—Clutch-size is 4 eggs (4.1, 3-6; 15).

Nests are placed from eight to 70 feet high (averaging 24 feet) in forks, crotches, and on horizontal limbs of elm, maple, osage orange, cottonwood, and ash.

Black-billed Magpie: *Pica pica hudsonia* (Sabine).—This resident is common in western Kansas, along riparian groves and woodland edge. Records of nesting are from as far east as Clay County. Wolfe (1961) outlines the history of magpies in Decatur County as follows: the species was purported to have appeared in rural districts near Oberlin in 1918, but Wolfe saw the birds only by 1921, at which time he also found the first (used) nests. The first reported occupied nest was one in Hamilton County in 1925 (Linsdale, 1926). Earlier records, chiefly of occurrence in winter, can be found in Goss (1891).

Breeding schedule.—Fourteen records of breeding span the period April 11 to June 20; the modal date for egg-laying is May 15.

Number of eggs.—There are no data on clutch-size in Kansas; elsewhere Black-billed Magpies lay 3 to 9 eggs, and clutches of 7 are found most frequently (Linsdale, 1937:104).

Nests are placed from 10 to 18 feet high (averaging 13 feet) in forks or lateral masses of branches in cottonwood, box elder, ash, and willow.

White-necked Raven: *Corvus cryptoleucus* Couch.—This summer resident is common in western Kansas, probably occupying locally favorable sites in prairie grassland and woodland edge west of a line from Smith to Seward counties. The species is known to nest in Cheyenne, Sherman, and Finney counties.

Breeding schedule.—There are few data from Kansas; Aldous (1942) states that the birds begin activities leading to building sometime in April in Oklahoma; the peak of egg-laying probably occurs in May, which coincides with the records from Kansas.

Number of eggs.—Outside Kansas, this species lays 3 to 7 eggs; these figures seem applicable to Kansas, where brood sizes are known to run from 1 to 7 young.

Nests are placed about 20 feet high in cottonwood and other trees.

Common Crow: *Corvus brachyrhynchos brachyrhynchos* Brehm.—This resident is common in most of Kansas, but numbers are lower in the west. Distribution in the breeding season is west at least to Cheyenne, Logan, and Meade counties.

Breeding schedule.—Sixty-nine records of breeding span the period March 10 to May 31 (Fig. 7); the modal date for egg-laying is April 5, and 60 per cent of all eggs are laid between March 21 and April 10.

Number of eggs.—Clutch-size is 4 eggs (4.2, 3-5; 19).

Nests are placed about 20 feet high in crotches near trunks or heavy branches of such trees as red cedar, elm, oak, osage orange, cottonwood, honey locust, box elder, and pine.

Black-capped Chickadee: *Parus atricapillus* Linnaeus.—This resident is common north of the southernmost tier of counties, in forested and wooded areas. *P. a. atricapillus* Linnaeus occurs chiefly east of the 98th meridian, and *P. a. septentrionalis* Harris occurs west of this; a broad zone of intergradation exists between these two subspecies.

Breeding schedule.—Fifty-one records of breeding span the period March 21 to June 10 (Fig. 7); the modal date for laying is April 15, and 64 per cent of all eggs are laid between April 11 and 30.

Number of eggs.—Clutch-size is 5 eggs (5.4, 4-7; 10).

Nests are placed in cavities about ten feet high (ranging from four to 20 feet) in willow, elm, cottonwood, honey locust, apricot, or nestboxes placed by man.

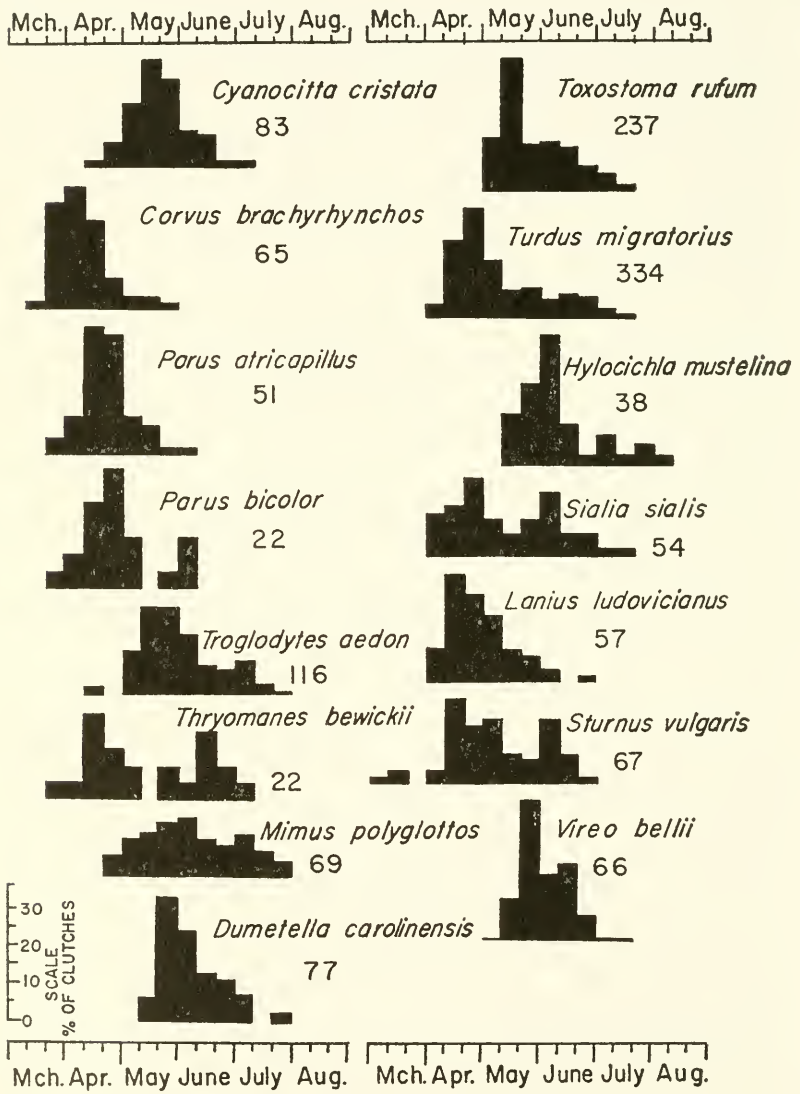

FIG. 7.—Histograms representing breeding schedules of crows, chickadees, wrens, thrashers, thrushes, and their allies in Kansas. See legend to Figure 1 for explanation of histograms.

Carolina Chickadee: *Parus carolinensis atricapilloides* Lunk.—This resident is common in the southernmost tier of counties, from Comanche County east, in forest and woodland edge. Actual records of breeding are from Barber and Montgomery counties.

Breeding schedule.—There are no data on breeding of this species in Kansas.

Number of eggs.—Clutch-size is about 5 eggs.

Nests are placed in cavities of trees.

Tufted Titmouse: *Parus bicolor* Linnaeus.—This resident is common in the eastern half of Kansas, in woodlands. Specimens taken in the breeding season and nesting records come from east of a line running through Cloud, Harvey, and Sumner counties, and the species probably breeds in Barber County.

Breeding schedule.—Twenty-two records of breeding span the period March 21 to June 10 (Fig. 7); the modal date for laying is April 25, and 54 per cent of all clutches are laid in the period April 11 to 30.

Number of eggs.—Clutch-size is 4 to 5 eggs (4.5; 6).

Nests are placed in cavities about 12 feet high (ranging from three to 30 feet) in elm, oak, cottonwood, hackberry, redbud, osage orange, and nestboxes placed by man.

White-breasted Nuthatch: *Sitta carolinensis* Latham.—This resident in eastern Kansas, in well-developed woodland, is uncommon. *S. c. cookei* Oberholser occurs east of a line running through Douglas and Cherokee counties, on the basis of specimens taken in the breeding season and actual nesting records, and *S. c. carolinensis* Latham occurs in Montgomery and Labette counties. *S. c. nelsoni* Mearns has been recorded in Morton County but probably does not breed there.

Breeding schedule.—Eggs are laid in March and April; young have been recorded being fed by parents throughout May.

Number of eggs.—Clutch-size is between 5 and 10 eggs.

Nests are placed in cavities about 30 feet high in elm and sycamore.

House Wren: *Troglodytes aedon parkmanii* Audubon.—This summer resident is common in the east and uncommon in the west. Preferred habitat is in woodland, brushland, and urban parkland. House Wrens arrive in eastern Kansas in the period April 3 to 27 (the median is April 19), and are last seen in autumn in the period September 19 to October 13 (the median is September 30).

Breeding schedule.—The 116 records of breeding span the period April 11 to July 31 (Fig. 7); the modal date of laying is May 20. About 45 per cent of all clutches are laid in the period May 11 to 31.

Number of eggs.—Clutch-size is 7 eggs (5.8, 3-7; 20). Clutches laid in May average 6.1 eggs (4-7; 14); those laid in June and July average 5.0 eggs (3-7; 6).

Nests are placed in cavities about ten feet high (ranging from two to 50 feet) in cottonwood, elm, willow, and a wide variety of structures, mostly nestboxes, built by man.

Bewick Wren: *Thryomanes bewickii* Audubon.—This wren is an uncommon resident in Kansas, except for the northeastern quarter, in woodland under-

story and brushland. *T. b. bewickii* Audubon occurs north and east of stations in Riley, Pottawatomie, Douglas, and Linn counties, and *T. b. cryptus* Oberholser is found south of stations in Greeley, Stafford, and Linn counties; a zone of intergradation occurs between the two named populations. The species occupies marginal habitat in most of Kansas and periodically is reduced in numbers by severe winters.

Breeding schedule.—Twenty-two records of breeding span the period March 21 to July 10 (Fig. 7); the modal date for first clutches is April 15 and for second clutches June 15.

Number of eggs.—Clutch-size is 5 eggs (5.5, 5-7; 12).

Nests are placed in crevices about five feet high (ranging from zero to nine feet) in trees (oak, cherry, and pear), boulders, and a wide variety of structures, some of them nestboxes, built by man; appropriation and modification of nests of Barn Swallows is known to occur.

Carolina Wren: *Thryothorus ludovicianus ludovicianus* Latham.—This common resident of southeastern Kansas in woodland understory and brushland is uncommon in the northeastern and south-central sectors. Stations of breeding all fall east of a line running through Doniphan, Riley, and western Reno counties. North and west of southeastern Kansas the Carolina Wren is in marginal habitat and periodically is reduced in numbers by severe winters.

Breeding schedule.—Fourteen records of breeding span the period April 11 to August 10; the modal date for laying is April 15, to judge only from the present sample. The species probably breeds also in late March and early April.

Number of eggs.—Clutch-size is 4 eggs (4.2, 3-8; 9).

Nests are placed near the ground in stumps, and a wide variety of structures built by man, or in crevices in earthen banks.

Long-billed Marsh Wren: *Telmatodytes palustris dissaëptus* (Bangs).—This is an uncommon summer resident in eastern Kansas in and around marshes. Presumably breeding individuals occur east of stations in Doniphan, Shawnee, and Sedgwick counties, but actual records of breeding come only from Doniphan County (Linsdale, 1928:505). First dates of arrival in spring run from April 19 to 29 (the median is April 22), and dates of last autumnal occurrence are from September 26 to October 31 (the median is October 8).

Breeding schedule.—Eggs are laid from May to August.

Number of eggs.—Clutch-size is 5 or 6 eggs; the range is from 3 to 10 (Welter, 1935).

Nests are woven of broad-bladed grasses, usually no farther than two feet from water or mud, suspended in vertical plant stalks or branches in marshes.

Short-billed Marsh Wren: *Cistothorus platensis stellaris* (Nauman).—This rare and irregular summer resident in northeastern Kansas occurs in wet meadowland. Breeding records are available from Douglas and Coffey counties. Temporal occurrence in the State is at least from April 29 to October 25; early dates are most likely of transients.

Breeding schedule.—Eggs are laid in late July and August.

Number of eggs.—Clutch-size is 6 or 7 eggs.

Nests are woven of plant fibers and placed in vertically-running stalks and stems of grasses and short, woody vegetation, within two feet of the ground.

Rock Wren: *Salpinctes obsoletus obsoletus* (Say).—This species is a common summer resident in western Kansas, in open, rocky country. Specimens taken in the breeding season and actual nests found come from west of stations in Decatur, Trego, and Comanche counties. Dates of occurrence are from April 2 to October 25. Autumnal, postbreeding movement brings the species east at least to Cloud County (October 7, 8, and 12) and Douglas County (October 25).

Breeding schedule.—Sixteen records of breeding span the period May 11 to July 20; the modal date for egg-laying is June 15.

Number of eggs.—Clutch-size is 5 eggs (4.6, 3-7; 5).

Nests are placed in holes in rocks, occasionally in rodent burrows, from ground level to 80 feet high on faces of cliffs, but there averaging about 20 feet.

Northern Mockingbird: *Mimus polyglottos* (Linnaeus).—This is a common resident in parkland and brushy savannah throughout Kansas. *M. p. polyglottos* (Linnaeus) occurs in the east, and *M. p. leucopterus* (Vigors) in the west; a broad zone of intergradation exists between the two. Most specimens from Kansas are of intermediate morphology.

Breeding schedule.—Sixty-nine records of breeding span the period April 21 to July 31 (Fig. 7); the modal date for first clutches is June 5, but is weakly indicated in the histogram (Fig. 7).

Number of eggs.—Clutch-size is 3 eggs (3.5, 3-5; 27). Size of clutch does not vary seasonally or geographically in the present sample.

Nests are placed about four feet high (two to 10 feet) in osage orange, red cedar, mulberry, scotch pine, catalpa, cottonwood, rose, and arbor vitae.

Catbird: *Dumetella carolinensis* (Linnaeus).—This is a common summer resident in the eastern half of Kansas, but is local in the west, in and near woodland edge and second-growth. First dates of arrival in spring are from April 25 to May 14 (the median is May 6), and last dates of autumnal occurrence are between September 20 and November 16 (the median is September 26).

Breeding schedule.—Seventy-seven records of breeding span the period May 11 to July 31 (Fig. 7); the modal date for egg-laying is May 25, and 57 per cent of all clutches are laid from May 21 to June 10.

Number of eggs.—Clutch-size is 4 eggs (3.3, 2-5; 43). Clutches laid between May 11 and June 10 tend to be of 4 eggs (3.5, 2-5; 27), and clutches laid between June 11 and July 31 tend to be of 3 eggs (2.9, 2-4; 16).

Nests are placed about four feet high in shrubs (rose, lilac, plum, elderberry) and about seven feet high in trees (red cedar, honey locust, willow, elm, apple, and in vines in such trees).

Brown Thrasher: *Toxostoma rufum* (Linnaeus).—This is a common summer resident in woodland understory, edge, and second-growth. *T. r. rufum* (Linnaeus) occurs in eastern Kansas, to the western edge of the Flint Hills, and *T. r. longicauda* Baird occurs west of stations in Decatur, Lane, and Meade counties; the intervening populations are of intermediate morphologic character. Some individuals overwinter in Kansas, but most are regular migrants and summer residents, arriving in spring from April 1 to April 25 (the

median is April 19), and departing in autumn between September 19 and October 13 (the median is September 28).

Breeding schedule.—The 237 records of breeding span the period May 1 to July 20 (Fig. 7); the modal date for egg-laying is May 15, and one-third of all eggs are laid in the period May 11 to 20.

Number of eggs.—Clutch-size is 4 eggs, ranging from 2 to 5. Seasonal variation and mean values are shown in Table 15.

TABLE 15.—SEASONAL VARIATION IN CLUTCH-SIZE OF THE BROWN THRASHER

TIME	Mean clutch-size	Number of records
May 1–10	3.3	15
May 10–20	3.9	38
May 21–31	4.1	13
June 1–10	3.5	13
June 11–20	3.5	12
June 21–30	3.4	9
July 1–10	3	1
July 11–20	3	1
All:	3.63	102

Nests are placed about four feet high (ranging from 1⅔ to 15 feet) in osage orange, elm, ornamental evergreens, gooseberry, barberry, honey locust, cottonwood, red cedar, rose, plum, honeysuckle, spirea, arbor vitae, willow, oak, apple, dogwood, and maple.

Robin: *Turdus migratorius migratorius* Linnaeus.—This summer resident is common in the east, and is locally common in the west. Some individuals, usually in small groups, can be seen throughout the winter in eastern Kansas, and their presence makes it difficult to document dates of arrival and departure of the strictly summer resident birds; these can be said to arrive in March and to leave in October, but these indications are the barest approximations.

Breeding schedule.—The 334 records of breeding span the period April 1 to July 20 (Fig. 7); the modal date of laying of first clutches is April 25, but subsequent peaks are indistinct. Nearly half of all eggs are laid in the period April 11 to 30.

Number of eggs.—Clutch-size is 3 eggs (3.6,3-6; 57). Clutches laid prior to May 10 average 3.6 eggs (3-6; 47), and those laid subsequent to May 10 average 3.5 eggs (3-4; 10).

Nests are placed about 13 feet from the ground (ranging from two to 30 feet) in elm, ornamental conifers, fruit trees, cottonwood, mulberry, walnut, hackberry, oak, ash, maple, osage orange, and coffeeberry. Robins rarely nest in manmade structures, such as on rafters in sheds and barns, on bridge stringers, and, exceptionally, on electrical utility pole installations.

Wood Thrush: *Hylocichla mustelina* (Gmelin).—This is an uncommon summer resident in eastern Kansas, presently absent from the State west of stations in Cloud and Barber counties. Preferred habitat is found in understory of forest and woodland. Wood Thrushes appear to have nested in small numbers as far west as Oberlin, Decatur County (Wolfe, 1961), some 50 years ago, but have since disappeared from such places, probably as a result

of progressive modification of watershed and riparian timber by man. First dates of arrival in spring are from April 19 to May 20 (the median is May 9), and departure southward is in the period September 3 to October 1 (the median is September 15).

Breeding schedule.—Thirty-eight records of breeding fall in the period May 11 to August 10 (Fig. 7); the modal date of egg-laying is June 5 for first clutches. Fifty-five per cent of all eggs are laid between May 21 and June 10.

Number of eggs.—Clutch-size is 3 eggs (3.4, 3-4; 9).

Nests are placed about 11 feet high in elm, dogwood, willow, linden, and oak.

Eastern Bluebird: *Sialia sialis sialis* (Linnaeus).—This locally common resident and summer resident in eastern Kansas, is only casual west of Comanche County, in open parkland and woodland edge.

Breeding schedule.—Fifty-four records of breeding span the period April 1 to July 20 (Fig. 7); the modal date for first clutches is April 25 and for second clutches is June 5.

Number of eggs.—Clutch-size is 5 eggs (4.9, 4-6; 15).

Nests are placed in cavities about eight feet high in trees (elm, box elder, fruit trees, willow, and ash), and about four feet high in stumps, fence posts, and nestboxes placed by man.

Blue-gray Gnatcatcher: *Polioptila caerulea caerulea* (Linnaeus).—This summer resident is common in eastern Kansas in brushy woodland, edge, and second growth. Specimens taken in the breeding season and nesting records come from east of stations in Riley and Cowley counties, but there is a breeding specimen from Oklahoma just south of Harper County, Kansas. The species is present from March 30 to September 18.

Breeding schedule.—Twelve records of breeding span the period April 20 to June 20; the modal date for egg-laying is May 10.

Number of eggs.—Clutch-size is about 5 eggs.

Nests are placed in forks or on limbs about 17 feet high in oak, elm, honey locust, red haw, pecan, and walnut.

Cedar Waxwing: *Bombycilla cedrorum* Vieillot.—This waxwing is a rare, local, and highly irregular summer resident in northeastern Kansas, in woodland and forest edge habitats. The known nesting stations are in Wyandotte and Shawnee counties; six nests have been found in the period 1949 to 1960. The species has been recorded in all months.

Breeding schedule.—Eggs are laid in June and early July.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898).

Nests are placed four to 24 feet high in a variety of deciduous and coniferous trees and shrubs.

Loggerhead Shrike: *Lanius ludovicianus* Linnaeus.—This common resident and summer resident favors open country with scattered shrubs and thickets. *L. l. migrans* Palmer occurs in eastern Kansas, west to about the 96th meridian, and *L. l. excubitorides* Grinnell occurs in western Kansas, east to about the 100th meridian; populations of intermediate character occupy central Kansas. These shrikes tend to be resident in southern counties, but are migratory in the north. Dates of spring arrival in Cloud County are between March 9 and

31 (the median is March 21) and the birds leave southward between October 19 and December 19 (the median is November 1).

Breeding schedule.—Fifty-seven records of breeding span the period April 1 to June 30 (Fig. 7); the modal date for egg-laying is April 15.

Number of eggs.—Clutch-size is 5 eggs (5.3, 4-7; 32). There is no seasonal variation in the sample.

Nests are placed about six feet high (ranging from four to 10 feet) in osage orange, small pines, honeysuckle vines, and elm.

Starling: *Sturnus vulgaris* Linnaeus.—This species is a common resident in towns and around farms, foraging in open fields of various kinds. Starlings (introduced into North America from European stocks of *S. v. vulgaris*) first appeared in eastern Kansas in the early 1930s and were established as successful residents by 1935 or 1936. Occupancy of Kansas to the west took only a few years. There are no specimens taken in the breeding season or actual nesting records from southwest of Ellis and Stafford counties; Starlings seem to be resident in Cheyenne County, but no nesting record exists from there.

Breeding schedule.—Sixty-seven records of breeding span the period March 1 to June 30 (Fig. 7); the modal date for first clutches is April 15, and for second clutches is June 5.

Number of eggs.—Clutch-size is 5 eggs (5.2, 4-8; 19).

Nests are placed about 22 feet high (ranging from eight to 50 feet) in crevices in elm, locust, hackberry, nestboxes placed by man, and in a variety of other structures of man.

Black-capped Vireo: *Vireo atricapilla* Woodhouse.—This was a summer resident, apparently of limited distribution but in good numbers, in Comanche County, in oak woodland and brushland edge. No specimens have been taken in Kansas since 1885.

Breeding schedule.—Eggs are probably laid in May and June. Goss (1891: 351) found a nest under construction on May 11, 1885, and this is the only nesting record of the species in the State.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898).

Nests are placed low, perhaps around four feet high, in deciduous trees and shrubs (Davie, *op. cit.*).

White-eyed Vireo: *Vireo griseus noveboracensis* (Gmelin).—This is a local summer resident in eastern Kansas, in woodland and forest edge. Stations of breeding occurrence are in Doniphan, Douglas, Johnson, Anderson, Labette, and Montgomery counties. The species is present within the extreme dates of April 23 to October 5 (Table 16).

Breeding schedule.—Ten records of breeding span the period May 10 to June 30; the modal date for egg-laying is June 10. The present sample is not adequate to indicate extreme or modal dates with reasonable accuracy.

Number of eggs.—Clutch-size is 4 eggs (3.6, 3-4; 5).

Nests are placed relatively low in forks in trees and shrubs.

Bell Vireo: *Vireo bellii bellii* Audubon.—This summer resident is common in riparian thickets and second-growth scrub. Temporal occurrence is indicated in Table 16.

Breeding schedule.—Sixty-six records of breeding span the period May 1 to July 20 (Fig. 7); the modal date for egg-laying is May 25, and a little under 40 per cent of all eggs are laid in the period May 21-31. Renesting following disruption of first nests is regular, and the small peak in the histogram in the period June 11-20 is representative of this.

Number of eggs.—Clutch-size is 4 eggs (4.6, 3-6; 21). Clutches in May have an average of 3.7 eggs, and those in June and July 3.6 eggs.

Nests are placed about two feet high (ranging from one to five feet) in terminal or lateral forks of small branches in elm, hackberry, osage orange, coralberry, dogwood, plum, honey locust, mulberry, willow, cottonwood, and box elder.

Yellow-throated Vireo: *Vireo flavifrons* Vieillot.—This is a rare and local summer resident in deciduous forest and woodland in eastern Kansas. Stations of breeding occurrence fall east of Shawnee and Woodson counties. Temporal occurrence is indicated in Table 16.

Breeding schedule.—Eggs are laid at least in May.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed 16 to 30 feet high in forks of mature deciduous trees.

Red-eyed Vireo: *Vireo olivaceus olivaceus* (Linnaeus).—This summer resident is common in the east, but is local and less abundant in the west, in woodland and deciduous forest. Temporal occurrence is indicated in Table 16.

TABLE 16.—OCCURRENCE IN TIME OF SUMMER RESIDENT VIREOS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
White-eyed Vireo	Apr. 23–May 25	May 8	Oct. 5	.....
Bell Vireo	Apr. 14–May 20	May 8	Aug. 26–Sept. 27	Sept. 6
Yellow-throated Vireo	Apr. 27–May 22	May 7	Aug. 23–Oct. 1	Aug. 31
Red-eyed Vireo	Apr. 21–May 10	May 4	Sept. 2–Oct. 7	Sept. 10
Warbling Vireo	Apr. 20–May 9	Apr. 28	Sept. 2–Oct. 6	Sept. 9

Breeding schedule.—Eight records of breeding fall in the period May 21 to July 31; most records of egg-laying are in the first week of June.

Number of eggs.—Clutch-size is 4 eggs (4.0, 3-5; 5).

Nests are placed in forks of mature deciduous trees, usually fairly high—perhaps 15 to 25 feet (Davie, 1898).

Warbling Vireo: *Vireo gilvus gilvus* (Vieillot).—This summer resident is common in woodland and forest edge. Temporal occurrence is indicated in Table 16.

Breeding schedule.—Seventeen records of breeding span the period May 1 to June 20, but it is likely that breeding later in June and July will be recorded. The modal date for egg-laying is June 5, and this seems to be a reliable index to the major effort in egg-laying in spite of the small sample.

Number of eggs.—Clutch-size is 4 eggs (3.6, 3-4; 5).

Nests are placed three to 25 feet high in a variety of deciduous shrubs and trees.

Black-and-white Warbler: *Mniotilta varia* (Linnaeus).—This local and uncommon summer resident lives in deciduous forest and woodland. Specimens taken in the breeding season and actual records of nesting come from Doniphan, Douglas, Coffey, Greenwood, Sedgwick, Labette, and Cherokee counties. Temporal occurrence in the State is indicated in Table 17.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is around 5 eggs (Davie, 1898).

Nests are placed on the ground, in depressions or niches, under heavy cover.

Prothonotary Warbler: *Protonotaria citrea* (Boddaert).—This is a local summer resident in eastern Kansas, in understory of riparian timber and swampy woodland. Specimens taken in the breeding season and actual records of nesting come from Doniphan, Douglas, Linn, and Cowley counties. Temporal occurrence is indicated in Table 17.

Breeding schedule.—Twenty-two records of breeding span the period May 11 to July 10 (Fig. 8); the modal date for egg-laying is June 5, and 75 per cent of all clutches are laid in the period June 1 to 20.

Number of eggs.—Clutch-size is 5 eggs (4.5, 3-6; 15).

Nests are placed in holes and niches in willow, red haw, elm, and a variety of stumps, about eight feet high (ranging from five to 20 feet), usually over water. A pair nested once in a gourd under the eave of a house in Winfield, Cowley County, and another pair in a tin cup on a shelf at a sawmill (Goss, *ex* Long, 1936).

Parula Warbler: *Parula americana* (Linnaeus).—This summer resident in eastern Kansas usually can be found in heavy woodland and flood-plain timber. Specimens taken in the breeding season and actual records of breeding come from Doniphan, Riley, Douglas, Montgomery, Labette, and Cherokee counties. Temporal occurrence is indicated in Table 17.

Breeding schedule.—Eggs are laid at least from mid-May to mid-June.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed in debris in root tangles along stream banks, and, presumably, in pendant arboreal lichens.

Yellow Warbler: *Dendroica petechia* (Linnaeus).—This summer resident is common in the east, in woodland and riparian growths. *D. p. aestiva* (Gmelin) occupies eastern Kansas west at least to Barber County, but it is not known how far west representatives of this population breed. *D. p. morcomi* Coale breeds in western Kansas. *D. p. sonorana* Brewster, a name applicable to Yellow Warblers of the southwestern United States and northern Mexico, has been considered a "straggler" (Long, 1940) or probable summer resident (Tordoff, 1956; Johnston, 1960) in southwestern Kansas, on the basis of one specimen taken on June 24, 1911, at a point two miles south of Wallace, Wallace County. This specimen, which is pale, was identified in 1935 as *D. p. sonorana* by H. C. Oberholser. Specimens taken subsequently from Cheyenne, Hamilton, and Morton counties in the breeding season can be referred adequately to *D. p. morcomi*. Probably the specimen of 1911 is a pale variant of *D. p. morcomi* within its normal distributional range.

Breeding schedule.—Thirty-five records of breeding span the period May 11 to June 20 (Fig. 8); this probably is inadequate to show the extent of the season, and some egg-laying into July is likely to be found in the future. The modal date of egg-laying is May 25, and this is likely to be reliable.

Number of eggs.—Clutch-size is 4 eggs (4.2, 3-5; 29).

Nests are placed about nine feet high (ranging from five to 20 feet) in crotches of trees and shrubs including willow, elderberry, cottonwood, crab-apple, plum, and coralberry.

Prairie Warbler: *Dendroica discolor discolor* (Vieillot).—This rare, local summer resident occurs in deciduous second-growth. The only breeding records are from Wyandotte and Johnson counties.

Breeding schedule.—Eggs are laid at least in June.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898).

Nests are placed low, perhaps about four feet high, in a wide variety of small trees and shrubs.

Louisiana Waterthrush: *Seiurus motacilla* (Vieillot).—This uncommon to rare summer resident in eastern Kansas lives in woodland understory near streams. Nesting records come from Douglas, Miami, Linn, and Crawford counties. Wolfe (1961) reports he found a nest with young near Oberlin, Decatur County, on June 10, 1910, under an overhanging bank of Sappa Creek; Decatur County is some 250 miles west of the present western limit of the breeding range of the Louisiana Waterthrush, and western habitats are not favorable for their occurrence. Temporal characteristics of their distribution are indicated in Table 17.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is about 5 eggs (Davie, 1898).

Nests are placed in concealed places in banks or stumps always where it is wet.

TABLE 17.—OCCURRENCE IN TIME OF SUMMER RESIDENT WOOD WARBLERS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Black-and-white Warbler	Apr. 2–May 12	May 5	Sept. 10–Oct. 14	Sept. 22
Prothonotary Warbler	Apr. 24–May 25	May 8	Aug. 6–Sept. 10	Aug. 22
Parula Warbler	Apr. 6–May 5	Apr. 23	Sept. 12–Oct. 7	Sept. 18
Yellow Warbler	Apr. 21–May 7	Apr. 30	Aug. 28–Oct. 1	Sept. 4
Louisiana Waterthrush	Apr. 2–May 2	Apr. 16	Aug. ?	.....
Kentucky Warbler	Apr. 24–May 15	May 3	Sept. 13	.....
Yellowthroat	Apr. 21–May 10	May 3	Sept. 8–Oct. 3	Sept. 17
Yellow-breasted Chat	Apr. 29–May 19	May 11	Aug. 29–Oct. 1	Sept. 8
American Redstart	Apr. 22–May 20	May 12	Sept. 1–Oct. 7	Sept. 10

Kentucky Warbler: *Oporornis formosus* (Wilson).—This is an uncommon summer resident in eastern Kansas, in deciduous forest and woodland. Specimens taken in the breeding season and actual records of nesting come from Riley, Doniphan, Douglas, Leavenworth, Linn, Montgomery, and Labette counties. Temporal occurrence is indicated in Table 17.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is 4 or 5 eggs.

Nests are placed near or on the ground, usually at the base of small shrubs or clumps of grass.

Yellowthroat: *Geothlypis trichas* (Linnaeus).—This summer resident in and near marshes is common in the east and is local and somewhat less common in the west. *G. t. brachydactylus* (Swainson) breeds east of stations in Clay, Greenwood, and Montgomery counties, *G. t. occidentalis* Brewster breeds west of stations in Decatur, Stafford, and Pratt counties, and the intervening area is occupied by warblers of intermediate morphologic characters. Temporal occurrence is indicated in Table 17.

Breeding schedule.—Nine records of breeding span the period May 11 to June 10; the modal date of egg-laying is June 1. The season is probably more extended in time than is indicated by the available records.

Number of eggs.—Clutch-size is 5 eggs (4.8, 4-5; 6).

Nests are placed in cattails and sedges one to two and one-half feet high.

Yellow-breasted Chat: *Icteria virens* (Linnaeus).—This summer resident is common in willow thickets and rank second-growth. *I. v. virens* (Linnaeus) breeds in eastern Kansas, from Nemaha County south, *I. v. auricollis* (Deppe) breeds in western Kansas, from Norton County south, and the intervening sector is occupied by chats of intermediate morphologic character. Temporal occurrence is indicated in Table 17.

Breeding schedule.—Twenty-six records of breeding span the period May 11 to July 20 (Fig. 8); the modal date for completion of clutches is June 5. Forty-two per cent of all eggs are laid in the period June 1 to 10.

Number of eggs.—Clutch-size is 4 eggs (3.9, 3-5; 21). Clutches in May are larger than those in June and July.

Nests are placed in forks and crotches about three feet high in dogwood, willow, rose, coralberry, cottonwood, and thistles.

Hooded Warbler: *Wilsonia citrina* (Boddaert).—This warbler is a rare summer resident in eastern Kansas, in wet, open woodland. Specimens (a total of four) taken in the breeding season are from Leavenworth and Shawnee counties, and the one nesting record is from Anderson County.

Breeding schedule.—Eggs are laid at least in May.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are low (some as high as six feet) in woody vegetation.

American Redstart: *Setophaga ruticilla ruticilla* (Linnaeus).—This summer resident occurs locally in woodlands east from stations in Cloud and Sumner Counties. Temporal occurrence is indicated in Table 17.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898), but there are two records of 5 in Kansas.

Nests are placed six to 30 feet high, but usually about 12 feet, in forks or saddled on a branch, in deciduous trees.

House Sparrow: *Passer domesticus* (Linnaeus).—This sparrow, introduced from stocks in Ohio and New York (originally from England and Germany), has been present since about 1876 in eastern Kansas; it is a common resident in towns and at farmsteads throughout the state.

Nomenclaturally, House Sparrows in North America consistently have been

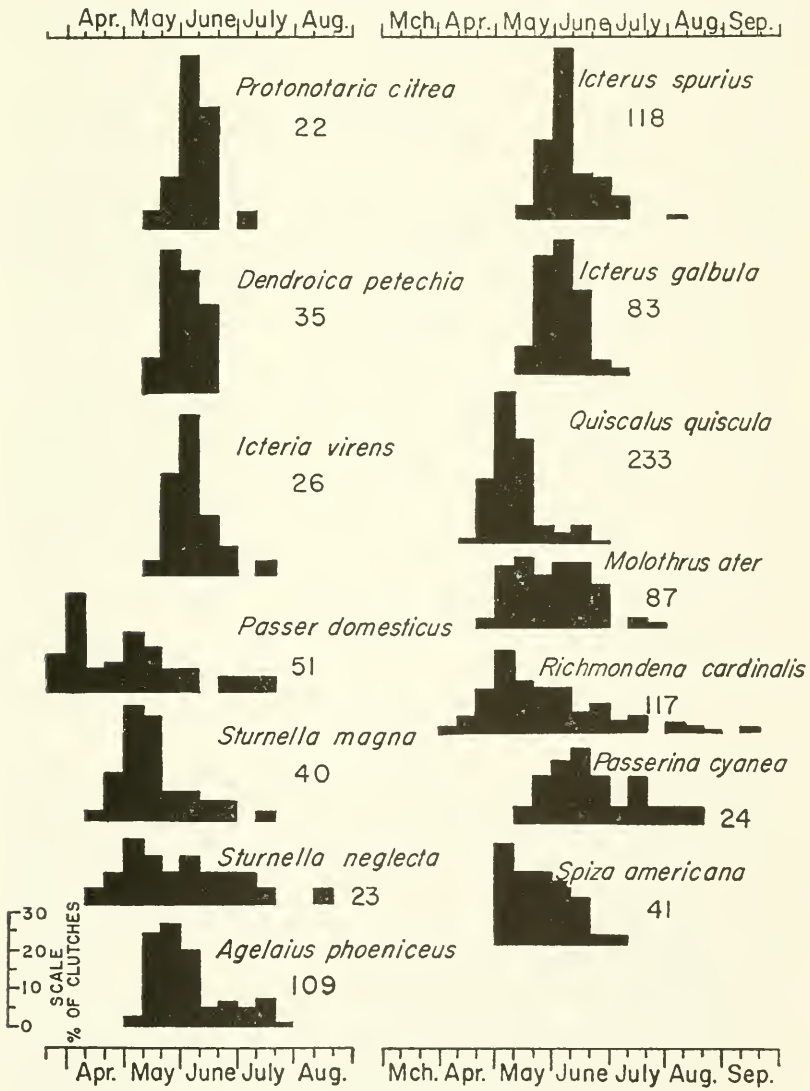

FIG. 8.—Histograms representing breeding schedules of wood warblers, the House Sparrow, icterids, and cardinal grosbeaks in Kansas. See legend to Figure 1 for explanation of histograms.

referred to the European ancestral stocks, *P. d. domesticus,* but none in North America today duplicates morphologically the European birds. This is evidence of meaningful adaptation of the North American populations to environments in which they now live, and continued use of *P. d. domesticus* in misleading. Studies on local differentiation in North American House Sparrows are in progress, and when the biology of sparrows in the midwest is better understood, suitable nomenclatural proposals will be made.

Breeding schedule.—Fifty-one records of breeding span the period March 20 to July 20 (Fig. 8); the modal date for laying of first clutches is April 5, and for second clutches May 5.

Number of eggs.—Clutch-size is 4 eggs (3.9, 3-7; 13).

Nests are placed in niches of various sorts seven to 50 feet high in buildings, nestboxes, and trees, or freely situated in forks and crotches of large trees.

Bobolink: *Dolichonyx oryzivorus* (Linnaeus).—This species is a rare and local summer resident, in and about grassy meadows. There are but two stations of breeding in Kansas: Jamestown State Lake, Cloud County, and Big Salt Marsh, Stafford County. Temporal occurrence is indicated in Table 18.

Breeding schedule.—Eggs are laid in June.

Number of eggs.—Clutch-size is about 5 eggs.

Nests are placed on the ground amidst grasses.

Eastern Meadowlark: *Sturnella magna* (Linnaeus).—This summer resident and resident is common in eastern Kansas, in moist grassland. *S. m. argutula* Bangs occurs in Montgomery, Labette, and Cherokee counties and intergrades to the north and west with *S. m. magna* (Linnaeus). Good numbers of birds are found east of the Flint Hills, but to the west the species is of restricted and local distribution. Extreme outliers of the species are found no farther west than stations in Jewell, Stafford, and Barber counties.

Breeding schedule.—Forty records of breeding span the period April 10 to July 20 (Fig. 8); the modal date for egg-laying is May 5. Fifty-seven per cent of all eggs are laid in the period May 1 to 20.

Number of eggs.—Clutch-size is 5 eggs (5.2, 4-7; 26). Prior to May 11, clutch-size is 5.3 eggs (13 records), and after that date it is 5.1 eggs (13 records).

Nests are placed on the ground, with cover of grasses or forbs.

Western Meadowlark: *Sturnella neglecta neglecta* (Audubon).—This is a common resident and summer resident in western Kansas, and is restricted and local in the east; preferred habitat is in grassy uplands.

Breeding schedule.—Twenty-three records of breeding span the period April 10 to July 30 (Fig. 8); the modal date for egg-laying is May 5 for first nests and June 5 for second nests.

Number of eggs.—Clutch-size is 4 eggs (4.3, 3-6; 16).

Nests are placed on the ground with cover of grasses or forbs.

Yellow-headed Blackbird: *Xanthocephalus xanthocephalus* (Bonaparte).—This uncommon and local summer resident occurs chiefly in the west, in marshes. Nesting records are from Wallace, Meade, Barton, Stafford, Doniphan, and Douglas counties. Temporal occurrence is indicated in Table 18.

Breeding schedule.—Fifty-one records of breeding span the period May 20

to June 30; the modal date of egg-laying is June 5. The sample is probably not large enough to be wholly reliable.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed within a few feet of water in cattail, rush, sedge, and willow.

Red-winged Blackbird: *Agelaius phoeniceus* (Linnaeus).—This is a common summer resident in marshes, wet pasture, and scrubby parkland throughout the State. *A. p. phoeniceus* (Linnaeus) occurs in most of Kansas and *A. p. fortis* (Ridgway) occurs in the west, east to about Decatur County. A few birds can be found in eastern Kansas in winter; the full breeding population is present between April and October.

Breeding schedule.—The 109 records of breeding in Cloud County span the period May 1 to July 30 (Fig. 8); the modal date for laying is May 25, and 71 per cent of all eggs are laid in the period May 11 to June 10. Eighty-eight records of breeding from northwestern Kansas make a histogram almost exactly duplicating the one from Cloud County.

Number of eggs.—Clutch-size at Concordia, Cloud County, is 4 eggs (3.7, 3-5; 48); in northeastern Kansas mean clutch-size is 3.7 eggs (3-5; 46). For the total sample, mean clutch-size in May is 4.0 eggs, in June, 3.7 eggs, and in July, 3.3 eggs.

Nests are placed about four feet high (one to nine feet) in willow, cattail, sedge, grass, elm, exotic conifer, elderberry, coralberry, buttonbrush, honeysuckle, smartweed, ash, osage orange, and yellow clover.

In central Kansas red-wings are host to the Brown-headed Cowbird in a frequency of one parasitized nest out of nine; in northeastern Kansas the ratio is 1:25.

TABLE 18.—OCCURRENCE IN TIME OF SUMMER RESIDENT ICTERIDS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Bobolink	May 4–May 21	May 11	Aug. 28–Oct. 1	Sept. 12
Yellow-headed Blackbird	Mar. 31–Apr. 29	Apr. 19	Sept. 19–Oct. 18	Sept. 24
Orchard Oriole	Apr. 25–May 14	May 4	Aug. 5–Sept. 15	Aug. 9
Baltimore Oriole	Apr. 24–May 5	Apr. 29	Sept. 6–Sept. 29	Sept. 10
Common Grackle	Mar. 2–Mar. 27	Mar. 17	Oct. 15–Nov. 14	Oct. 31

Orchard Oriole: *Icterus spurius* (Linnaeus).—This summer resident is common in parkland, woodland, and old second-growth. Temporal occurrence is indicated in Table 18.

Breeding schedule.—The 118 records of breeding span the period May 11 to August 10 (Fig. 8); the modal date for completion of clutches is June 5, and 45 per cent of all eggs are laid in the first ten days of June.

Number of eggs.—Clutch-size is 4 eggs (4.1, 3-6; 41). Clutches laid at the peak of the season average 4.3 eggs (3-6; 26), and replacement clutches average 3.8 eggs (3-4; 9).

Nests are hung about 15 feet high (ranging from six to 55 feet) in elm, cottonwood, hackberry, locust, catalpa, willow, alder, osage orange, walnut, pear, linden, and ash.

Baltimore Oriole: *Icterus galbula* (Linnaeus).—This common summer resident is most numerous in the east, in woodland and riparian timber. The species hybridizes freely with the Bullock Oriole in western Kansas, and individuals morphologically typical of Baltimore Orioles are rare west of the 100th meridian. Evidence of such hybridization can be found in specimens taken in eastern Kansas, but the linear nature of distribution along watercourses to the west restricts gene-flow, and evident hybrids are not yet conspicuous. Temporal occurrence is indicated in Table 18.

Breeding schedule.—Eighty-three records of breeding span the period May 11 to July 10 (Fig. 8); the modal date of egg-laying is June 5, and 66 per cent of all eggs are laid between May 21 and June 10.

Number of eggs.—Clutch-size is 4 eggs.

Nests are hung about 24 feet high (ranging from nine to 70 feet) in elm, cottonwood, sycamore, maple, and oak.

Bullock Oriole: *Icterus bullockii* (Swainson).—This summer resident is common in western Kansas in woodland and riparian situations. The species hybridizes freely with the Baltimore Oriole, and most Bullock Orioles in Kansas show evidence of such interbreeding. Almost all records of breeding come from west of the 100th meridian, but the species in recognizable form probably breeds locally at least as far east as Stafford County.

Breeding schedule.—Few nesting records are available, but these suggest that the breeding schedule of the Bullock Oriole resembles those of the preceding two species in Kansas.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are hung about 26 feet high (ranging from 10 to 50 feet) in cottonwood, elm, and other large trees.

Common Grackle: *Quiscalus quiscula versicolor* Vieillot.—This summer resident is common in parkland, and around towns and farms. Most individuals move out of Kansas in winter, and the temporal occurrence of these birds is indicated in Table 18.

Breeding schedule.—The 233 records of breeding span the period April 11 to June 30 (Fig. 8); the modal date for egg-laying is May 5, and two-thirds of all eggs are laid between May 1 and May 20.

Number of eggs.—Clutch-size is 5 eggs (4.5, 3-6; 33). Clutches laid at the peak of the season average 4.7 eggs (3-6; 21), and those laid as replacement clutches average 4.3 eggs (3-6; 12).

Nests are placed in forks and crotches about 22 feet high (ranging from six to 50 feet) in elm, red cedar, cottonwood, oak, box elder, and pine.

Brown-headed Cowbird: *Molothrus ater ater* (Boddaert).—Many individuals of this common summer resident overwinter in the southern part of the State and it is difficult to determine dates of arrival and departure in Kansas. Conspicuous abundance in the north covers the period April to October.

Breeding schedule.—The 141 instances of egg-laying span the period April 21 to July 20 (Fig. 8); the modal date of laying is May 15, and 53 per cent of all eggs are laid in the period May 11 to June 10. Inception of laying is

here fairly reliably indicated, but in exceptionally early springs laying does occur earlier; a few eggs were found on April 6, 1963, too late for incorporation into this report other than in this sentence.

Number of eggs.—Clutch-size in cowbirds is not readily determined. On the basis of ovarian examination of five females taken in mid-season, the birds here lay about five eggs at a time. There is no question that the birds are "double-brooded" in Kansas, and the season is sufficiently long for as many as five "clutches" to be laid by a given female.

Eggs are laid in nests of some forty species of birds in Kansas; 39 of these are passerines. No preference for any one species is detectable; the most frequently parasitized species are simply the common species, and these are the kinds for which nesting records are easily gathered by man. In the following list of host species, the names marked with an asterisk are the conspicuously parasitized species.

Mourning Dove, Eastern Kingbird, Eastern Phoebe,* Say Phoebe,* Acadian Flycatcher, Barn Swallow, Horned Lark, Carolina Wren, Rock Wren, Brown Thrasher,* Mockingbird, Catbird, Wood Thrush,* Eastern Bluebird, Yellow-throated Vireo, Bell Vireo,* White-eyed Vireo,* Parula Warbler, Yellow Warbler, Black-and-white Warbler, Kentucky Warbler, Louisiana Waterthrush, Yellow-breasted Chat, Yellowthroat, Eastern Meadowlark, Western Meadowlark, Red-winged Blackbird,* Orchard Oriole,* Cardinal,* Black-headed Grosbeak, Indigo Bunting,* Blue Grosbeak, Dickcissel,* Pine Siskin,* Rufous-sided Towhee,* Grasshopper Sparrow, Lark Sparrow,* Chipping Sparrow, Field Sparrow.*

Scarlet Tanager: *Piranga olivacea* (Gmelin).—This rare summer resident in northeastern Kansas occurs in deciduous forest and bottomland timber. Specimens taken in the breeding season and records of nesting come from Clay, Doniphan, Douglas, Wyandotte, Johnson, and Linn counties, but the species probably occupies the entire eastern third of the State. Dates of arrival in spring are from April 29 to May 25 (the median is May 11), and dates of departure in autumn are from August 4 to September 23 (the median is August 10).

Breeding schedule.—Six records of breeding fall in the period May 11 to June 20.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed 20 to 35 feet high in elm, linden, hickory, and walnut.

Summer Tanager: *Piranga rubra rubra* (Linnaeus).—This uncommon summer resident in eastern Kansas occurs in woodland. Specimens taken in the breeding season and records of nesting come from east of stations in Doniphan, Shawnee, and Montgomery counties. Dates of arrival in spring run from April 24 to May 18 (the median is April 29), and the species departs southward in September and October.

Breeding schedule.—Eleven records of egg-laying cover the period May 21 to July 20; the modal date for laying is June 5.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are situated ten to 20 feet high on horizontal limbs of large trees.

Cardinal: *Richmondena cardinalis cardinalis* (Linnaeus).—This species is a common resident in eastern Kansas, west to about the 99th meridian; west

of this line the species becomes local and uncommon to rare. Habitat in the east is found in woodland, edge, second-growth and open riparian timber, and in the west the species is restricted to riparian growths, chiefly along the Republican, Solomon, Smoky Hill, Arkansas, and Cimarron rivers, and their larger tributaries.

Breeding schedule.—The 117 records of breeding span the period April 1 to September 20 (Fig. 8); the modal date for laying of first clutches is May 1, subsequent to which breeding activity is regular but asynchronous.

Number of eggs.—Clutch-size is 3 eggs (3.5, 3-6; 65). Seasonal variation in clutch-size is as follows:

Date	Mean clutch-size	Number of records
April 1-20	3.0	6
April 21-May 10	3.8	25
May 11-May 31	3.3	15
June 1-June 20	3.6	11
June 21-July 20	3.3	7

Nests are placed about five feet high (ranging from 10 inches to 40 feet) in osage orange, elm, grape, rose, red cedar, coralberry, willow, cottonwood, gooseberry, oak, elderberry, box elder, arbor vitae, Lombardy poplar, Forsythia, pines, honeysuckle, wisteria, lilac, red haw, hickory, dogwood, and sycamore.

Rose-breasted Grosbeak: *Pheucticus ludovicianus* (Linnaeus).—This is a local and at times common summer resident in eastern Kansas, in woodland, edge, and riparian timber. Specimens taken in the breeding season and actual records of breeding come from Clay, Riley, Doniphan, Leavenworth, and Douglas counties. This species meets and hybridizes with the Black-headed Grosbeak west of the Flint Hills. Temporal occurrence in the State is indicated in Table 19.

Breeding schedule.—Eleven records of breeding span the period May 11 to July 10; the modal date for laying is probably June 5.

Number of eggs.—Clutch-size is 3 or 4 eggs.

Nests are placed in deciduous trees, in forks and crotches six to 30 feet high.

Black-headed Grosbeak: *Pheucticus melanocephalus melanocephalus* (Swainson).—This summer resident is common in western Kansas, chiefly along streams. Individuals referable to this species by sight records alone breed in fair numbers as far east as Cloud and Sedgwick counties, but to the east of these stations numbers are reduced, partly as a result of presumed competition with the Rose-breasted Grosbeak. Hybrids between these two grosbeaks are regularly produced. The easternmost record of breeding by this species is at St. Mary's, Pottawatomie County, where a male was seen as probably mated with a female Rose-breasted Grosbeak. Temporal occurrence is indicated in Table 19.

Breeding schedule.—Sixteen records of breeding span the period May 11 to July 10; the modal date for egg-laying is June 5.

Number of eggs.—Clutch-size is about 4 eggs (3.7, 3-4; 4).

Nests are placed about 12 feet high in a variety of deciduous trees.

Blue Grosbeak: *Guiraca caerulea* (Linnaeus).—This is a common to uncommon summer resident in most of Kansas, in brushland and streamside thickets. *G. c. caerulea* (Linnaeus) breeds in the east, east of stations in Douglas, Greenwood, and Cowley counties, and *G. c. interfusa* Dwight and

Griscom breeds in the west, west of stations in Cloud, Stafford, and Clark counties; a broad zone of intergradation exists between the two named populations. Temporal occurrence is indicated in Table 19.

TABLE 19.—OCCURRENCE IN TIME OF SUMMER RESIDENT CARDINAL GROSBEAKS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Rose-breasted Grosbeak	Apr. 25–May 5	May 2	Sept. 4–Oct. 1	Sept. 13
Black-headed Grosbeak	Apr. 26–May 11	May 5	Aug. 17–Sept. 18	Sept. 2
Blue Grosbeak	Apr. 25–May 26	May 13	Aug. 15–Sept. 3	Aug. 27
Indigo Bunting	Apr. 20–May 15	May 6	Aug. 23–Oct. 31	Oct. 1
Lazuli Bunting	May 5–May 24	May 10	.....	.....
Painted Bunting	Apr. 30–May 25	May 9	.....	.....
Dickcissel	Apr. 21–May 10	May 4	Sept. 7–Oct. 11	Sept. 18

Breeding schedule.—Seven records of breeding span the period May 21 to June 30; the modal date of laying seems to be in late May or early June.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed from three to 30 feet high in a variety of deciduous plants.

Indigo Bunting: *Passerina cyanea* (Linnaeus).—This summer resident is common in mixed-field and heavy brushland habitats. The species extends westerly, in riparian situations, in reduced numbers, ultimately meeting and hybridizing with the Lazuli Bunting. Specimens referrable to the Indigo Bunting have been taken as far west as Finney County, but most specimens from that far west show evidence of interbreeding with Lazuli Buntings. Temporal occurrence is indicated in Table 19.

Breeding schedule.—Twenty-four records of breeding span the period May 11 to August 20 (Fig. 8); the modal date for egg-laying is June 15.

Number of eggs.—Clutch-size is 3 eggs (3.1, 2-4; 17).

Nests are placed about three feet high (ranging from one to nine feet) in coralberry, sumac, thistle, sycamore sprouts, hickory sprouts, grape, elderberry, cottonwood, dogwood, ragweed, and grasses.

Lazuli Bunting: *Passerina amoena* (Say).—This uncommon summer resident of western Kansas occurs in edge habitats and streamside thickets. The one breeding record is from Morton County, and there is a breeding specimen taken at Sharon Springs, Wallace County. The species hybridizes with the Indigo Bunting in the western half of the State. Temporal occurrence in spring is indicated in Table 19.

Breeding schedule.—Eggs are laid in June and July.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898).

Nests are placed a few feet from the ground, probably much as are nests of the Indigo Bunting.

Painted Bunting: *Passerina ciris pallidior* Mearns.—This is an uncommon

summer resident in the southeastern third of Kansas, in edge habitats and streamside brush. Specimens taken in the breeding season and actual nesting records come from Douglas, Shawnee, Geary, Barber, and Crawford counties. Temporal occurrence in spring is indicated in Table 19.

Breeding schedule.—Eggs are laid in June and July.

Number of eggs.—Clutch-size is about 4 eggs (Davie, 1898).

Nests are placed in deciduous shrubs and trees.

Dickcissel: *Spiza americana* (Gmelin).—This species is a common summer resident in eastern Kansas and is local and irregular in the west, in grassland habitats. Temporal occurrence is indicated in Table 19.

Breeding schedule.—Forty-one records of breeding span the period May 1 to July 10 (Fig. 8); the modal date for egg-laying seems to be May 5, but the curiously abrupt inception of breeding described by this sample suggests that more records are needed to document fully the breeding schedule of this species. Breeding in April almost certainly will be found.

Number of eggs.—Clutch-size is about 4 eggs (4.1, 3-5; 14).

Nests are placed about two feet high (ranging from ground level to 12 feet) in grasses, osage orange, sedge, box elder, honey locust, clover, thistle, and blackberry.

Pine Siskin: *Spinus pinus pinus* (Wilson).—This irregular summer resident occurs locally north of the 38th parallel, chiefly around planted conifers. Known stations of breeding are in Hays, Ellis County, Concordia, Cloud County, and Onaga and St. Marys, Pottawatomie County.

Breeding schedule.—Twelve records of breeding span the period March 11 to May 20 (Fig. 9); most nests have been established in late April or by early May.

Number of eggs.—Clutch-size is about 4 eggs. Of ten nests examined for eggs, five had at least one egg of the Brown-headed Cowbird; if it is assumed that each cowbird egg replaced one of the siskins, mean clutch-size is 3.7 eggs.

Nests are placed about seven feet high (ranging from 3.5 to 13 feet) in red cedar, exotic conifers, and Lombardy poplar.

American Goldfinch: *Spinus tristis tristis* (Linnaeus).—This resident is common in woodland edge, scrubby second-growth, old fields, and riparian thickets. Occurrence tends to be local and at low density in the southwestern sector.

Breeding schedule.—Twelve records of breeding span the period June 20 to September 10 (Fig. 9); the modal date for laying is August 5.

Number of eggs.—Clutch-size is 4 eggs (4.4, 3-6; 8).

Nests are placed from two to eight feet high in woody or herbaceous vegetation.

Red Crossbill: *Loxia curvirostra* Linnaeus.—This is an uncommon and irregular winter visitant to Kansas, but it nested once in Shawnee County. *L. c. minor* (Brehm), on geographic grounds, probably nested here, but five other subspecies have been recorded in the State and any one of these might have undertaken the aberrant breeding.

Breeding record.—Three eggs, set completed March 24, 1917, Shawnee County; successfully fledged (Hyde, 1917:166).

The species usually lays 4 eggs and places its nests in conifers.

Rufous-sided Towhee: *Pipilo erythrophthalmus erythrophthalmus* (Linnaeus).—This is an uncommon summer resident in eastern Kansas, in understory of woodland and streamside timber. Specimens taken in the breeding season and actual records of nesting come from east of stations in Cloud, Marion, and Cherokee counties. Temporal occurrence is indicated in Table 20; records of *P. e. arcticus* (Swainson) have been eliminated from the sample as far as has been possible.

Breeding schedule.—Nineteen records of breeding span the period April 21 to August 10 (Fig. 9); the modal date for egg-laying is May 5.

Number of eggs.—Clutch-size is 4 eggs (4.0, 3-7; 14).

Nests are placed on the ground, in heavy cover.

Lark Bunting: *Calamospiza melanocorys* Stejneger.—This species is ordinarily a common summer resident in western Kansas, in grassland and open

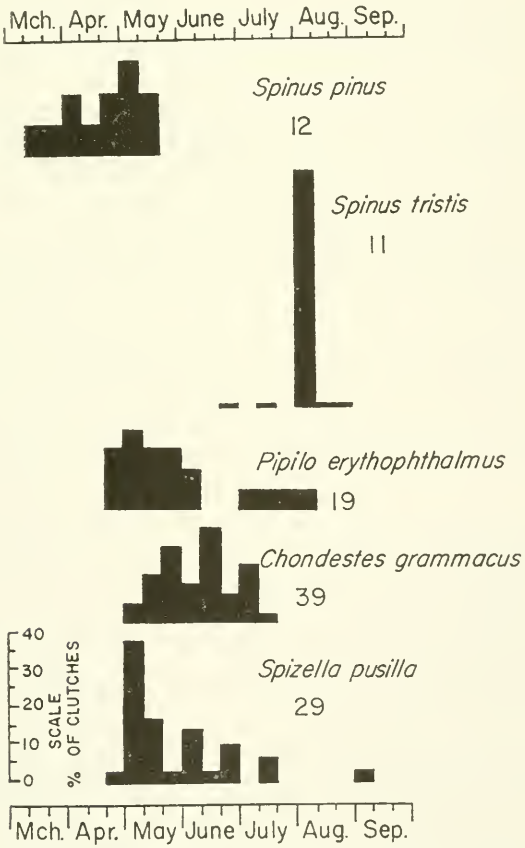

FIG. 9.—Histograms representing breeding schedules of cardueline and emberizine finches in Kansas. See legend to Figure 1 for explanation of histograms.

scrub. Specimens taken in the breeding season and all breeding records except one for western Franklin County come from west of stations in Decatur, Ellis, and Comanche counties. Irregular fluctuations in breeding density have been recorded from Decatur County (Wolfe, 1961). Temporal occurrence is indicated in Table 20.

Breeding schedule.—Fourteen records of breeding span the period May 21 to June 20; the modal date of egg-laying cannot be determined from the present sample.

Number of eggs.—Clutch-size is 4 eggs (4.1, 3-5; 7).

Nests are placed on the ground, at bases of clumps of grasses.

Grasshopper Sparrow: *Ammodramus savannarum perpallidus* (Coues).—This species is a local and at times common summer resident throughout Kansas, in grassland. Temporal occurrence is indicated in Table 20.

Breeding schedule.—Seven records of breeding fall in the period May 1 to June 30; the modal date of laying seems to be about May 21.

Number of eggs.—Clutch-size is 5 eggs (4.8, 4-5; 5).

Nests are placed on the ground or in low vegetation, with cover of grasses or forbs.

Henslow Sparrow: *Passerherbulus henslowii henslowii* (Audubon).—This is an uncommon and local summer resident in eastern Kansas, in grassland. Breeding records are from Cloud, Shawnee, Douglas, Morris, and Anderson counties. Temporal occurrence is indicated in Table 20.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is about 5 eggs.

Nests are placed on the ground, usually in bluestem pasture, but in any case grasses.

Lark Sparrow: *Chondestes grammacus* (Say).—This is a common summer resident in grassland edge habitats. *C. g. grammacus* (Say) breeds east of the Flint Hills, east of stations in Pottawatomie, Anderson, and Montgomery counties, and *C. g. strigatus* Swainson breeds west of stations in Clay, Dickinson, Harvey, and Sedgwick counties; specimens from the intervening area are of intermediate subspecific character. Temporal occurrence is indicated in Table 20.

Breeding schedule.—Thirty-nine records of breeding span the period May 1 to July 20 (Fig. 9); the modal date for egg-laying is probably May 25, but the sample may not be reliable in this respect.

Number of eggs.—Clutch-size is 4 eggs (4.1, 3-5; 28).

Nests are usually placed on the ground, in cover of pasture grasses, clover, thistle, milo maize, and soybean; there is one record of a nest one and one-half feet high in a small pine.

Cassin Sparrow: *Aimophila cassinii* (Woodhouse).—This is a common summer resident in open scrub and grassland edge, to the south and west of Wallace and Comanche counties. Specimens taken in the breeding season and actual nesting records are from Wallace, Hamilton, Kearny, Finney, Morton, and Comanche counties; the A. O. U. Check-list (1957) cites Hays, Ellis County, as a breeding locality, but it is doubtful that the species now occurs there.

Breeding schedule.—Eggs are laid in May and June.

Number of eggs.—Clutch-size is about 4 eggs.

Nests are placed on the ground, at bases of small bushes.

Chipping Sparrow: *Spizella passerina passerina* (Bechstein).—This is an uncommon summer resident in open woodland, second-growth, and edge.

TABLE 20.—OCCURRENCE IN TIME OF SUMMER RESIDENT AMERICAN BUNTINGS IN KANSAS

SPECIES	Arrival		Departure	
	Range	Median	Range	Median
Rufous-sided Towhee	Apr. 2–Apr. 19	Apr. 9	Sept. 20–Oct. 8	Sept. 29
Lark Bunting	May 5–May 14	May 10	.....	.....
Grasshopper Sparrow	Apr. 12–May 11	Apr. 29	Aug. 20–Oct. 6	Aug. 31
Henslow Sparrow	Apr. 14–Apr. 30	Apr. 22	Oct. 15	.....
Lark Sparrow	Mar. 29–Apr. 21	Apr. 18	Sept. 13–Oct. 16	Oct. 12
Chipping Sparrow	Mar. 6–Apr. 29	Apr. 23	Oct. 3–Nov. 15	Oct. 20
Field Sparrow	Mar. 4–Apr. 28	Apr. 7	Oct. 5–Nov. 12	Oct. 30

S. p. passerina is found east of stations in Barber and Shawnee counties; Chipping Sparrows are not known to breed farther to the west, but records for north-central Kansas are likely to be found. The subspecific affinities of our Chipping Sparrows are entirely with the nominate subspecies, and there is no basis for earlier reports (Long, 1940; Tordoff, 1956; Johnston, 1960) that *S. p. arizonae* Coues (=*S. p. boreophila* Oberholser) occurs in Kansas.

Breeding schedule.—Nine records of breeding fall in the period May 1 to May 10, in no way indicating the whole span of the breeding season; the species probably lays eggs in May and July, as well as in June.

Number of eggs.—Clutch-size is 4 eggs.

Nests are placed four to 40 feet high in evergreens of a variety of kinds.

Field Sparrow: *Spizella pusilla* (Wilson).—This species is a common summer resident in grassland and edge habitats. *S. p. pusilla* (Wilson) breeds in eastern Kansas chiefly east of the Flint Hills; *S. p. arenacea* Chadbourne breeds in central and western Kansas, intergrading easterly with *S. p. pusilla.*

Breeding schedule.—Twenty-nine records of breeding span the period April 21 to September 10 (Fig. 9); the modal date for first clutches is May 5.

Number of eggs.—Clutch-size is 4 eggs (4.1, 3-5; 21).

Nests are placed about 10 inches high (ranging from ground level to three feet) in or among coralberry, osage orange, elm, oak, rose, and, once, peony.

Chestnut-collared Longspur: *Calcarius ornatus* (Townsend).—This was formerly a summer resident in western Kansas, in short-grass habitat. The only known nesting area was in the vicinity of Ft. Hays, Ellis County. The species is to be looked for in prairie with short grass type of vegetation.

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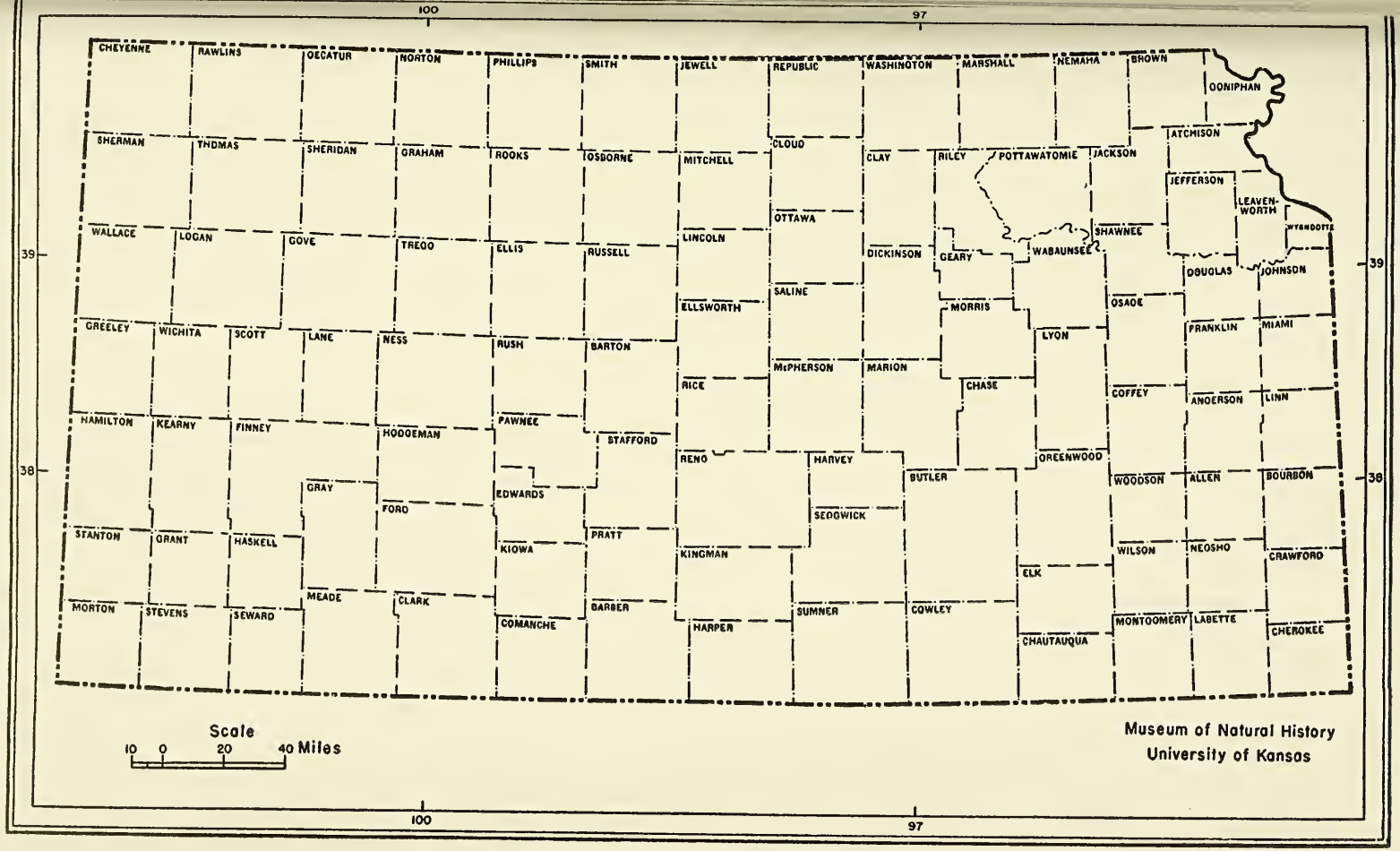

FIG. 10.—Map of Kansas showing names of counties.

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3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
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5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.
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The Adductor Muscles of the Jaw In Some Primitive Reptiles

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RICHARD C. FOX

Information about osteological changes in the groups of reptiles that gave rise to mammals is preserved in the fossil record, but the musculature of these reptiles has been lost forever. Nevertheless, a reasonably accurate picture of the morphology and the spatial relationships of the muscles of many of these extinct vertebrates can be inferred by studying the scars or other marks delimiting the origins and insertions of muscles on the skeletons of the fossils and by studying the anatomy of Recent genera. A reconstruction built by these methods is largely speculative, especially when the fossil groups are far removed in time, kinship and morphology from Recent kinds, and when distortion, crushing, fragmentation and overzealous preparation have damaged the surfaces associated with the attachment of muscles. The frequent inadequacy of such direct evidence can be partially offset by considering the mechanical demands that groups of muscles must meet to perform a particular movement of a skeletal member.

Both direct anatomical evidence and inferred functional relations were used to satisfy the purposes of the study here reported on. The following account reports the results of my efforts to: 1, reconstruct the adductor muscles of the mandible in *Captorhinus* and *Dimetrodon;* 2, reconstruct the external adductors of the mandible in the cynodont *Thrinaxodon;* and 3, learn the causes of the appearance and continued expansion of the temporal fenestrae among the reptilian ancestors of mammals.

The osteology of these three genera is comparatively well-known. Although each of the genera is somewhat specialized, none seems to have departed radically from its relatives that comprised the line leading to mammals.

I thank Prof. Theodore H. Eaton, Jr., for suggesting the study here reported on, for his perceptive criticisms regarding it, and for his continued patience throughout my investigation. Financial assistance was furnished by his National Science Foundation Grant (NSF-G8624) for which I am also appreciative. I thank Dr. Rainer Zangerl, Chief Curator of Geology, Chicago Museum of Natural History, for permission to examine the specimens of *Captorhinus*

and *Dimetrodon* in that institution. I am grateful to Mr. Robert F. Clarke, Assistant Professor of Biology, The Kansas State Teachers College, Emporia, Kansas, for the opportunity to study his specimens of *Captorhinus* from Richard's Spur, Oklahoma. Special acknowledgment is due Mr. Merton C. Bowman for his able preparation of the illustrations.

Captorhinus

The outlines of the skulls of *Captorhinus* differ considerably from those of the skulls of the primitive captorhinomorph *Protorothyris.* Watson (1954:335, Fig. 9) has shown that in the morphological sequence, *Protorothyris—Romeria—Captorhinus,* there has been flattening and rounding of the skull-roof and loss of the primitive "square-cut" appearance in transverse section. The quadrates in *Captorhinus* are farther from the midline than in *Protorothyris,* and the adductor chambers in *Captorhinus* are considerably wider than they were primitively. Additionally, the postorbital region of *Captorhinus* is relatively longer than that of *Protorothyris,* a specialization that has increased the length of the chambers within.

In contrast with these dimensional changes there has been little shift in the pattern of the dermal bones that roof the adductor chambers. The most conspicuous modification in *Captorhinus* is the absence of the tabular. This element in *Protorothyris* was limited to the occiput and rested without sutural attachment upon the squamosal (Watson, 1954:338); later loss of the tabular could have had no effect upon the origins of muscles from inside the skull roof. Changes in pattern that may have modified the origin of the adductors in *Captorhinus* were correlated with the increase in length of the parietals and the reduction of the supratemporals. Other changes that were related to the departure from the primitive romeriid condition of the adductors included the development of a coronoid process, the flattening of the quadrate-articular joint, and the development of the peculiar dentition of *Captorhinus.*

The adductor chambers of *Captorhinus* are large. They are covered dorsally and laterally by the parietal, squamosal, postfrontal, postorbital, quadratojugal and jugal bones. The chamber extends medially to the braincase, but is not limited anteriorly by a bony wall. The occiput provides the posterior limit. The greater part of the adductor chambers lies mediad of the mandibles and thus of the Meckelian fossae; consequently the muscles that arise from the dermal roof pass downward and outward to their insertion on the mandibular rami.

Mandible

The mandibular rami of *Captorhinus* are strongly constructed. Each ramus is slightly convex in lateral outline. Approximately the anterior half of each ramus lies beneath the tooth-row. This half is roughly wedge-shaped in its lateral aspect, reaching its greatest height beneath the short posterior teeth.

The posterior half of each ramus is not directly involved in supporting the teeth, but is associated with the adductor musculature and the articulation of the ramus with the quadrate. The ventral margin of this part of the ramus curves dorsally in a gentle arc that terminates posteriorly at the base of the retroarticular process. The dorsal margin in contrast sweeps sharply upward behind the teeth and continues posteriorly in a long, low, truncated coronoid process.

A prominent coronoid process is not found among the more primitive members of the suborder, such as *Limnoscelis*, although the mandible commonly curves upward behind the tooth-row in that genus. This area in *Limnoscelis* is overlapped by the cheek when the jaw is fully adducted (Romer, 1956:494, Fig. 213), thereby foreshadowing the more extreme condition in *Captorhinus*.

The coronoid process in *Captorhinus* is not oriented vertically, but slopes inward toward the midline at approximately 45 degrees, effectively roofing the Meckelian fossa and limiting its opening to the median surface of each ramus. When the jaw was adducted, the coronoid process moved upward and inside the cheek. A space persisted between the process and the cheek because the process sloped obliquely away from the cheek and toward the midline of the skull. The external surface of the process presented an area of attachment for muscles arising from the apposing internal surface of the cheek.

Palate

The palate of *Captorhinus* is of the generalized rhynchocephalian type (Romer, 1956:71). In *Captorhinus* the pterygoids and palatines are markedly arched and the relatively large pterygoid flange lies almost entirely below the lower border of the cheek. The lateral edge of the flange passes obliquely across the anterior lip of the Meckelian fossa and abuts against the bottom lip of the fossa when the jaw is closed.

The palatines articulate laterally with the maxillary bones by means of a groove that fits over a maxillary ridge. This presumably allowed the halves of the palate to move up and down rather freely. The greatest amplitude of movement was at the midline. Antero-

posterior sliding of the palate seems impossible in view of the firm palatoquadrate and quadrate-quadratojugal articulations.

The subtemporal fossa is essentially triangular, and its broad end is bounded anteriorly by the pterygoid flange. The fossa is lateral to much of the adductor chamber; consequently muscles arising from the parietals passed ventrolaterally, parallel to the oblique quadrate ramus of the pterygoid, to their attachment on the mandible.

Musculature

These osteological features indicate that the adductor muscles of the jaw in *Captorhinus* consisted of two primary masses (Figs. 1, 2, 3). The first of these, the capitimandibularis, arose from the internal surface of the cheek and roof of the skull and inserted on the bones of the lower jaw that form the Meckelian canal and the coronoid process.

The muscle was probably divided into a major medial mass, the temporal, and a lesser, sheetlike lateral mass, the masseter. The

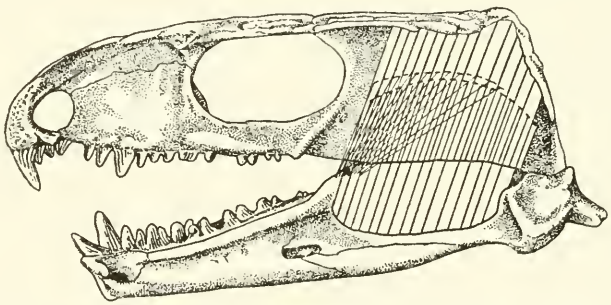

FIG. 1. *Captorhinus.* Internal aspect of skull, showing masseter, medial adductor, and temporal muscles. Unnumbered specimen, coll. of Robert F. Clarke. Richard's Spur, Oklahoma. × 2.

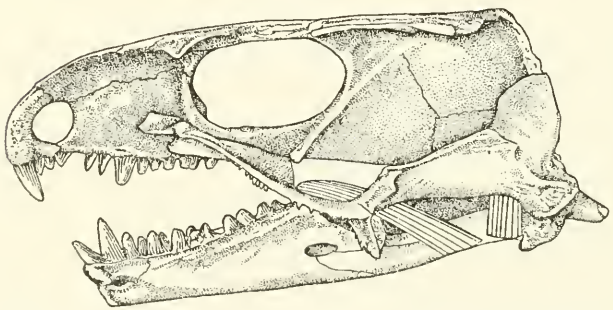

FIG. 2. *Captorhinus.* Internal aspect of skull, showing anterior and posterior pterygoid muscles. Same specimen shown in Fig. 1. × 2.

temporal was the largest of the adductors and arose from the lateral parts of the parietal, the dorsal parts of the postorbital, the most posterior extent of the postfrontal, and the upper parts of the squamosal. The muscle may have been further subdivided, but evidence for subordinate slips is lacking. The fibers of this mass were nearly vertically oriented in lateral aspect since the parts of the ramus that are available for their insertion lie within the anteroposterior extent of the adductor chamber. In anterior aspect the fibers were obliquely oriented, since the jaw and subtemporal fossa are lateral to much of the skull-roof from which the fibers arose.

The masseter probably arose from the quadratojugal, the jugal, and ventral parts of the squamosal, although scars on the quadratojugal and jugal are lacking. The squamosal bears an indistinct, gently curved ridge, passing upward and forward from the posteroventral corner of the bone and paralleling the articulation of the squamosal with the parietal. This ridge presumably marks the upper limits of the origin of the masseter from the squamosal.

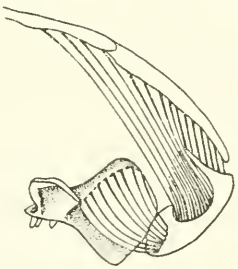

FIG. 3. *Captorhinus.* Cross-section of right half of skull immediately behind the pterygoid flange, showing masseter, temporal, and anterior pterygoid muscles. Same specimen shown in Fig. 1. × 2.

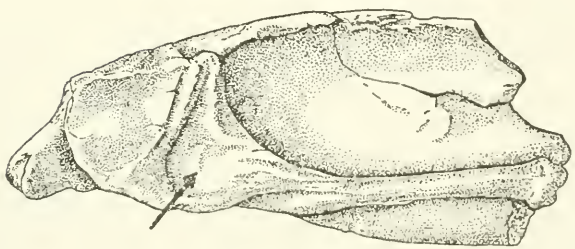

FIG. 4. *Captorhinus.* Internal aspect of left mandibular fragment, showing insertion of posterior pterygoid muscle. KU 8963, Richard's Spur, Oklahoma. × 2.8.

The masseter inserted on the external surface of the coronoid process, within two shallow concavities separated by an oblique ridge. The concavities and ridge may indicate that the muscle was divided into two sheets. If so, the anterior component was wedge-shaped in cross-section, and its thin posterior edge overlapped the larger mass that inserted on the posterior half of the coronoid process.

From a functional standpoint it is doubtful that a major component of the adductors arose from the quadrate wing of the pterygoid, for when the jaw is closed the Meckelian fossa is directly lateral to that bone. If the jaw were at almost any angle but maximum depression, the greatest component of force would be mediad, pulling the rami together and not upward. The mediad component would increase as the jaw approached full adduction. Neither is there anatomical evidence for an adductor arising from the quadrate wing of the pterygoid. The bone is smooth, hard, and without any marks that might be interpreted as muscle scars.

The internal adductor or pterygoid musculature in *Captorhinus* consisted of anterior and posterior components. The anterior pterygoid arose from the lateral edge and the dorsal surface of the pterygoid flange. The burred dorsal recurvature of the edge resembles that of the flange of crocodiles, which serves as part of the origin of the anterior pterygoid in those animals. In *Captorhinus* the attachment of the anterior pterygoid to the edge of the flange was probably tendinous, judging from the extent of the development of the edge of the flange. From the edge the origin extended medially across the dorsal surface of the flange; the ridging of this surface is indistinct, leading to the supposition that here the origin was more likely to have been fleshy than tendinous.

The anterior pterygoid extended obliquely backward and downward from its origin, passed medial to the temporal muscle and inserted on the ventral and medial surfaces of the splenial and angular bones beneath the Meckelian fossa. The spatial relationship between the palate and quadrate-articular joint indicate that the muscle was probably a minor adductor in *Captorhinus*.

When the jaw was adducted, the insertion of the anterior pterygoid was in a plane nearly level with the origin. Contraction of the anterior pterygoid when the jaw was in this position pulled the mandible forward and did not adduct it. Maximum depression of the mandible produced maximum disparity vertically between the levels of the origin and insertion. The force exerted by the anterior

pterygoid upon the mandible when fully lowered most nearly approached the perpendicular to the long axes of the mandibular rami, and the resultant force acting on the mandible was adductive.

The adductive component of force therefore decreased as the jaw swung upward, with the result that the anterior pterygoid could only have been active in initiating adduction and not in sustaining it.

The evidence regarding the position and extent of the posterior pterygoid is more veiled. On the medial surface of the mandible, the prearticular and articular bones meet in a ridge that ventrally rims the glenoid cavity (Fig. 4). The ridge extends anteriorly and curves slightly in a dorsal direction and meets the Meckelian fossa. The curved part of the ridge is made of the prearticular bone alone. A small hollow above the ridge, anterior to the glenoid cavity, faces the medial plane of the skull and is bordered by the articular bone behind and above, and by the Meckelian fossa in front.

The surfaces of the hollow and the prearticular-articular ridge bear tiny grooves and ridges that seem to be muscle scars. The entire area of the hollow and its bordering features was probably the area of insertion of the posterior pterygoid.

However, the area of insertion lies mostly ventral to the articulating surface of the articular bone and extends but slightly in front of it. Seemingly little lever effect could be exercised by an adductor attaching in this position, namely, at the level of the fulcrum of the mandibular ramus.

The posterior pterygoid muscle probably arose from the anterior portion of the pterygoid wing of the quadrate, from a ridge on the ventromedial surface. From the relationship of the muscle to the articulation of the jaw with the skull, it may be deduced that the muscle was limited in function to the stabilization of the quadrate-articular joint by keeping the articular surfaces in close contact with each other and by preventing lateral slipping.

Finally there is evidence for an adductor between the temporal and masseter masses. The anterior dorsal lip of the Meckelian fossa supports a small knob to which this muscle attached, much as in *Sphenodon* (Romer, 1956:18, Fig. 12). Presumably the muscle was sheetlike and attached to the skull roof, medial to the attachment of the masseter.

A pseudotemporal may have been present, but evidence to indicate its extent and position is lacking. The muscle usually arises from the epipterygoid and nearby areas of the braincase and skull roof and inserts in the anterior parts of the fossa of the jaw. In *Captorhinus* the lateral wing of the pterygoid cuts across the fossa,

effectively blocking it from the upper and medial parts of the skull, the areas of origin for the pseudotemporal.

Dimetrodon

The morphology of the skull of *Dimetrodon* closely resembles that of the primitive *Haptodus* (Haptodontinae, Sphenacodontidae), and "hence may be rather confidently described as that of the family as a whole" (Romer and Price, 1940:285). The major differences between the two genera are in the increased specialization of the dentition, the shortening of the lacrimal, and the development of long vertebral spines in *Dimetrodon.* The absence of gross differences in the areas of the skull associated with the groups of muscles with which this study is concerned, implies a similarity in the patterns of musculature between the two groups. Romer and Price suggest that *Haptodus,* although too late in time to be an actual ancestor, shows "all the common features of the *Dimetrodon* group on the one hand and the therapsids on the other." The adductors of the jaw of *Dimetrodon* were probably little changed from those of the Haptodontinae and represent a primitive condition within the suborder.

Dimetrodon and *Captorhinus* differ in the bones associated with the adductor mechanism; the area behind the orbit in *Dimetrodon* is relatively shorter, reducing the comparative longitudinal extent of the adductor chamber. Furthermore, the dermal roof above the adductor chamber slopes gently downward from behind the orbit to its contact with the occipital plate in *Dimetrodon.* Temporal fenestrae are, of course, present in *Dimetrodon.*

Musculature

The adductor musculature of the lower jaw in *Dimetrodon* was divided into lateral and medial groups (Figs. 5, 6). The lateral division consisted of temporal and masseter masses. The temporal arose from the upper rim of the temporal opening, from the lateral wall of the skull behind the postorbital strut, and from the dorsal roof of the skull. The bones of origin included jugal, postorbital, postfrontal, parietal and squamosal. This division may also have arisen from the fascia covering the temporal opening (Romer and Price, 1940:53). The muscle passed into the Meckelian fossa of the mandible and inserted on the angular, surangular, prearticular, coronoid and dentary bones. Insertion on the lips of the fossa also probably occurred.

The lateral division arose from the lower rim of the temporal opening and from the bones beneath. Insertion was in the

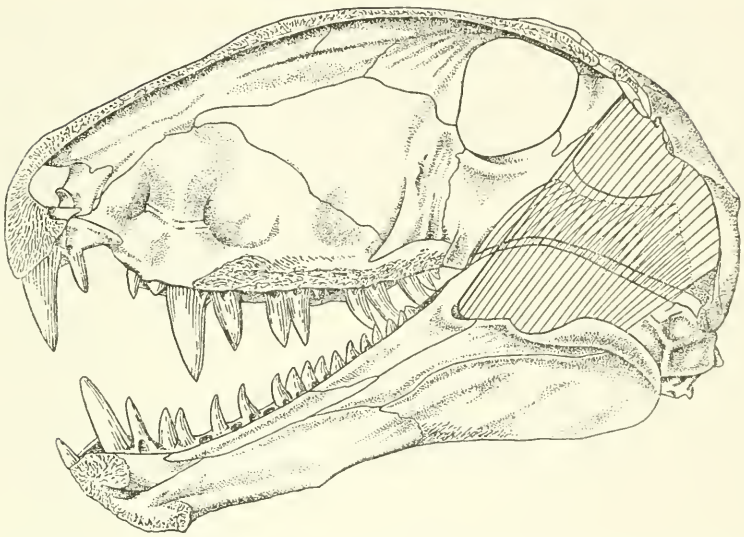

FIG. 5. *Dimetrodon.* Internal aspect of skull, showing masseter and temporal muscles. Skull modified from Romer and Price (1940). Approx. × ¼.

Meckelian fossa and on the dorsal surface of the adjoining coronoid process.

The reconstruction of the progressively widening masseter as it traveled to the mandible follows from the progressively widening depression on the internal wall of the cheek against which the muscle must have been appressed. The depressed surface included the posterior wing of the jugal, the whole of the squamosal, and probably the anteriormost parts of the quadratojugal. Expansion of the muscle rostrally was prevented by the postorbital strut that protected the orbit (Romer and Price, 1940:53).

The sphenacodonts possess the primitive rhynchocephalian kind of palate. In *Sphenodon* the anterior pterygoid muscle arises from the dorsal surface of the pterygoid bone and from the adjacent bones. A similar origin suggests itself for the corresponding muscle, the second major adductor mass, in *Dimetrodon.*

From the origin the muscle passed posterodorsad and laterad of the pterygoid flange. Insertion was in the notch formed by the reflected lamina of the angular, as suggested by Watson (1948).

In *Dimetrodon* the relationship of the dorsal surface of the palate and the ventromedial surface of the mandible in front of the articulation with the quadrate is unlike that in *Captorhinus.* When the mandible of *Dimetrodon* is at rest (adducted), a line drawn be-

tween these two areas is oblique, between 30 and 40 degrees from the horizontal. Depression of the mandible increases this angle. The insertion of the anterior pterygoid is thus always considerably below the origin, permitting the muscle to be active throughout the movement of the mandible, from maximum depression to complete adduction. This was a major factor in adding substantially to the speed and power of the bite.

The presence and extent of a posterior pterygoid is more difficult to assess, because of the closeness of the glenoid cavity and the raised ridge of the prearticular, and the occupancy of at least part of this region by the anterior pterygoid. In some specimens of *Dimetrodon* the internal process of the articular is double (see Romer and Price, 1940:87, Fig. 16) indicating that there was a double insertion here. Whether the double insertion implies the insertion of two separate muscles is, of course, the problem. Division of the pterygoid into anterior and posterior portions is the reptilian pattern (Adams, 1919), and such is adhered to here, with the posterior pterygoid arising as a thin sheet from the quadrate wing of the pterygoid and the quadrate, and inserting by means of a tendon on the internal process of the articular, next to the insertion of the anterior pterygoid.

Watson (1948) has reconstructed the musculature of the jaw in *Dimetrodon* with results that are at variance with those of the present study. Watson recognized two divisions, an inner temporal

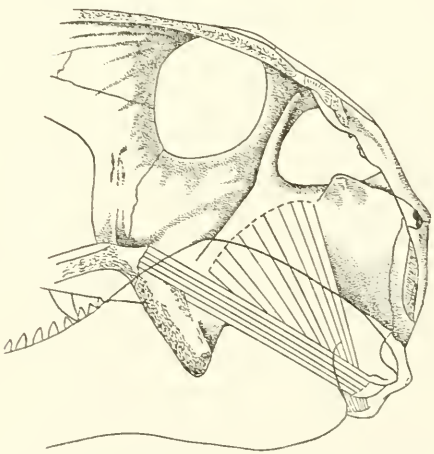

Fig. 6. *Dimetrodon.* Internal aspect of right cheek, showing anterior and posterior pterygoid muscles. Skull modified from Romer and Price (1940). Approx. × ¼.

and an outer masseteric, of the capitimandibularis, but has pictured them (830: Fig. 4; 831: Fig. 5C) as both arising from the inner surface of the skull roof above the temporal opening. But in *Captorhinus* the masseter arose from the lower part of the cheek close to the outer surface of the coronoid process. Watson has shown (1948:860, Fig. 17B) the same relationship of muscle to zygoma in *Kannemeyeria sp.* It is this arrangement that is also characteristic of mammals and presumably of *Thrinaxodon.* In view of the consistency of this pattern, I have reconstructed the masseter as arising from the lower wall of the cheek beneath the temporal opening.

Watson's reconstruction shows both the temporal and masseter muscles as being limited anteroposteriorly to an extent only slightly greater than the anteroposterior diameter of the temporal opening. The whole of the posterior half of the adductor chamber is unoccupied. More probably this area was filled by muscles. The impress on the inner surface of the cheek is evident, and the extent of both the coronoid process and Meckelian opening beneath the rear part of the chamber indicate that muscles passed through this area.

Watson remarked (1948:829-830) that the Meckelian opening in *Dimetrodon* "is very narrow and the jaw cavity is very small. None the less, it may have been occupied by the muscle or a ligament connected to it. Such an insertion leaves unexplained the great dorsal production of the dentary, surangular and coronoid. This may merely be a device to provide great dorsal-ventral stiffness to the long jaw, but it is possible and probable that some part of the temporal muscle was inserted on the inner surface of the coronoid. Indeed a very well-preserved jaw of *D. limbatus*? (R. 105: Pl. I, Fig. 2) bears a special depressed area on the outer surface of the extreme hinder end of the dentary which differs in surface modelling from the rest of the surface of the jaw, has a definite limit anteriorly, and may represent a muscle insertion. The nature of these insertions suggests that the muscle was already divided into two parts, an outer masseter and an inner temporalis." But, unaccountably, Watson's illustration (1948:830, Fig. 4) of his reconstruction limits the insertion of the temporal to the anterior limit of the Meckelian opening and a part of the coronoid process above it. No muscle is shown entering the Meckelian canal. It seems more likely that the temporal entered and inserted in the canal and on its dorsal lips. The masseter inserted lateral to it, over the peak of the coronoid process, and overlapping onto the dorsalmost portions of

its external face, as Watson has illustrated (Plate I, middle fig.).

I am in agreement with Watson's reconstruction of the origins for both the anterior and posterior pterygoid muscles. On a functional basis, however, I would modify slightly Watson's placement of the insertions of these muscles. Watson believed that the jaw of *Dimetrodon* was capable of anteroposterior sliding. The articular surfaces of the jaws of *Dimetrodon* that I have examined indicate that this capability, if present at all, was surely of a very limited degree, and in no way comparable to that of *Captorhinus*. The dentition of *Dimetrodon* further substantiates the movement of the jaw in a simple up and down direction. The teeth of *Dimetrodon* are clearly stabbing devices; they are not modified at all for grinding and the correlative freedom of movement of the jaw that that function requires in an animal such as *Edaphosaurus*. Nor are they modified to parallel the teeth of *Captorhinus*. The latter's diet is less certain, but presumably it was insectivorous (Romer, 1928). With the requisite difference in levels of origin and insertion of the anterior pterygoid in *Dimetrodon* insuring the application of force throughout the adduction of the jaws, it would seem that the whole of the insertion should be shifted downward and outward in the notch. If this change were made in the reconstruction, the anterior pterygoid would have to be thought of as having arisen by a tendon from the ridge that Watson has pictured (1948:828, Fig. 3) as separating his origins for anterior and posterior pterygoids. The posterior pterygoid, in turn, arose by tendons from the adjoining lateral ridge and from the pterygoid process of Romer and Price. Tendinous origins are indicated by the limitations of space in this area, by the strength of the ridges pictured and reported by Watson, and by the massiveness of the pterygoid process of Romer and Price.

Discussion

A comparison of the general pattern of the adductor musculature of *Captorhinus* and *Dimetrodon* reveals an expected similarity. The evidence indicates that the lateral and medial temporal masses were present in both genera. The anterior pterygoid aided in initiating adduction in *Captorhinus,* whereas in *Dimetrodon* this muscle was adductive throughout the swing of the jaw. Evidence for the presence and extent of a pseudotemporal muscle in both *Captorhinus* and *Dimetrodon* is lacking. The posterior division of the pterygoid is small in *Captorhinus.* In *Dimetrodon* this muscle has been reconstructed by Watson as a major adductor, an arrangement that is adhered to here with but slight modification.

The dentition of *Captorhinus* suggests that the jaw movement in feeding was more complex than the simple depression and adduction that was probably characteristic of *Dimetrodon* and supports the osteological evidence for a relatively complex adductor mechanism.

In *Captorhinus* the presence of an overlapping premaxillary beak bearing teeth that are slanted posteriorly requires that the mandible be drawn back in order to be depressed. Conversely, during closure, the jaw must be pulled forward to complete full adduction. The quadrate-articular joint is flat enough to permit such anteroposterior sliding movements. The relationship of the origin and insertion of the anterior pterygoid indicates that this muscle, ineffective in maintaining adduction, may well have acted to pull the mandible forward, in back of the premaxillary beak, in the last stages of adduction. Abrasion of the sides of the inner maxillary and outer dentary teeth indicates that tooth-to-tooth contact did occur. Whether such abrasion was due to contact in simple vertical adduction or in anteroposterior sliding is impossible to determine, but the evidence considered above indicates the latter probability.

Similarities of *Protorothyris* to sphenacodont pelycosaurs in the shape of the skull and palate already commented upon by Watson (1954) and Hotton (1961) suggest that the condition of the adductors in *Dimetrodon* is a retention of the primitive reptilian pattern, with modifications mainly limited to an increase in size of the temporalis. *Captorhinus*, however, seems to have departed rather radically from the primitive pattern, developing specializations of the adductors that are correlated with the flattening of the skull, the peculiar marginal and anterior dentition, the modifications of the quadrate-articular joint, and the development of the coronoid process.

Thrinaxodon

The evidence for the position and extent of the external adductors of the lower jaw in *Thrinaxodon* was secured in part from dissections of *Didelphis marsupialis*, the Virginia opossum. Moreover, comparison of the two genera reveals striking similarities in the shape and spatial relationships of the external adductors. These are compared below in some detail.

The sagittal crest in *Thrinaxodon* is present but low. It arises immediately in front of the pineal foramen from the confluence of bilateral ridges that extend posteriorly and medially from the base of the postorbital bars. The crest diverges around the foramen,

reunites immediately behind it, and continues posteriorly to its junction with the supraoccipital crest (Estes, 1961).

In *Didelphis* the sagittal crest is high and dorsally convex in lateral aspect, arising posterior to and medial to the orbits, reaching its greatest height near the midpoint, and sloping down to its termination at the supraoccipital crest. Two low ridges extend posteriorly from the postorbital process to the anterior end of the sagittal crest and correspond to ridges in similar position in *Thrinaxodon.*

The supraoccipital crest flares upward to a considerable extent in *Thrinaxodon* and slopes posteriorly from the skull-roof proper. The crest extends on either side downward to its confluence with the zygomatic bar. The area of the crest that is associated with the temporal musculature is similarly shaped in *Didelphis.*

The zygomatic bar in each genus is stout, laterally compressed, and dorsally convex on both upper and lower margins. At the back of the orbit of *Thrinaxodon,* the postorbital process of the jugal extends posterodorsally. At this position in *Didelphis,* there is but a minor upward curvature of the margin of the bar.

In *Thrinaxodon* the dorsal and ventral postorbital processes, arising from the postorbital and jugal bones respectively, nearly meet but remain separate. The orbit is not completely walled off from the adductor chamber. The corresponding processes in *Didelphis* are rudimentary so that the confluence of the orbit and the adductor chamber is complete.

The adductor chamber dorsally occupies slightly less than half of the total length of the skull of *Thrinaxodon;* in *Didelphis* the dorsal length of the chamber is approximately half of the total length of the skull.

The coronoid process in *Thrinaxodon* sweeps upward posterodorsally at an angle oblique to the long axis of the ramus. Angular, surangular and articular bones extend backward beneath and

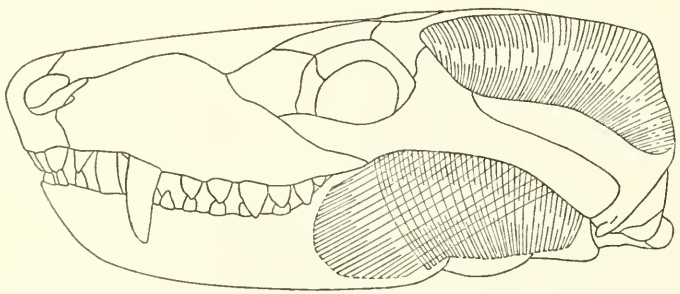

FIG. 7. *Thrinaxodon.* Showing masseter and temporal muscles. Skull after Romer (1956). Approx. × 7/10.

medial to the process. The process extends above the most dorsal point of the zygomatic bar, as in *Didelphis*. The mandibular ramus is ventrally convex in both genera.

The relationships described above suggest that *Thrinaxodon* and the therapsids having similar morphology in the posterior region of the skull possessed a temporal adductor mass that was split into major medial and lateral components (Fig. 7). The more lateral of these, the masseter, arose from the inner surface and lower margin of the zygomatic bar and inserted on the lateral surface of the coronoid process.

The medial division or temporal arose from the sagittal crest and supraoccipital crest and the intervening dermal roof. The muscle inserted on the inner and outer surfaces of the coronoid process and possibly on the bones beneath.

Thrinaxodon represents an advance beyond *Dimetrodon* in several respects. The zygomatic bar in *Thrinaxodon* extends relatively far forward, is bowed outward and dorsally arched. Consequently, the masseter was able to extend from an anterodorsal origin to a posterior and ventral insertion. The curvature of the jaw transforms the anterodorsal pull of the muscle into a dorsally directed adductive movement regardless of the initial angle of the jaw. This is the generalized mammalian condition.

With the development of the secondary palate the area previously available for the origin of large anterior pterygoid muscles was reduced. The development of the masseter extending posteroventrally from an anterior origin presumably paralleled the reduction of the anterior pterygoids. The therapsid masseter, as an external muscle unhindered by the crowding of surrounding organs, was readily available for the many modifications that have been achieved among the mammals.

In the course of synapsid evolution leading to mammals, the temporal presumably became the main muscle mass acting in adduction of the lower jaw. Its primacy is reflected in the phyletic expansion of the temporal openings to permit greater freedom of the muscles during contraction. In the synapsids that lead to mammals, there is no similar change in the region of the palate that can be ascribed to the effect of the pterygoid musculature, even though these adductors, like the temporal, primitively were subjected to severe limitations of space.

Didelphis

Dissections reveal the following relationships of the external adductors of the jaw in *Didelphis marsupialis* (Fig. 8).

1. MASSETER
   Origin: ventral surface of zygomatic arch.
   Insertion: posteroventral and lateroventral surface of mandible.
2. EXTERNAL TEMPORALIS
   Origin: sagittal crest; anteriorly with internal temporalis from frontal bone; posteriorly with internal temporalis from interparietal bone.
   Insertion: lateral surface of coronoid process of mandible.
3. INTERNAL TEMPORALIS
   Origin: sagittal crest and skull roof, including posterior two-thirds of frontal bone, whole of parietal, and dorsalmost portions of squamosal and alisphenoid.
   Insertion: medial surface of coronoid process; dorsal edge of coronoid process.

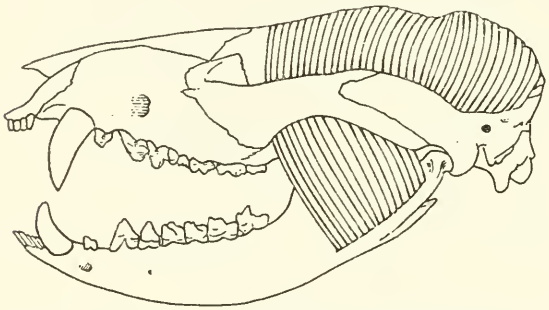

FIG. 8. *Didelphis marsupialis*. Showing masseter and temporal muscles. Skull KU 3780, 1 mi. N Lawrence, Douglas Co., Kansas. × ⅔.

Temporal Openings

In discussions of the morphology and functions of the adductor mechanism of the lower jaw, the problem of accounting for the appearance of temporal openings in the skull is often encountered. Two patterns of explanation have evolved. The first has been the attempt to ascribe to the constant action of the same selective force the openings from their inception in primitive members of a phyletic line to their fullest expression in terminal members. According to this theory, for example, the synapsid opening appeared *originally* to allow freer expansion of the adductor muscles of the jaw during contraction, and continued selection for that character caused the openings to expand until the ultimately derived therapsid or mammalian condition was achieved.

The second course has been the attempt to explain the appearance of temporal openings in whatever line in which they occurred by the action of the same constant selective force. According to the reasoning of this theory, temporal fenestration in all groups was

due to the need to decrease the total weight of the skull, and selection in all those groups where temporal fenestration occurs was to further that end.

Both of these routes of inquiry are inadequate. If modern views of selection are applied to the problem of explaining the appearance of temporal fenestrae, the possibility cannot be ignored that:

1. Selective pressures causing the inception of temporal fenestrae differed from those causing the continued expansion of the fenestrae.
2. The selective pressures both for the inception and continued expansion of the fenestrae differed from group to group.
3. Selection perhaps involved multiple pressures operating concurrently.
4. Because of different genotypes the potential of the temporal region to respond to selective demands varied from group to group.

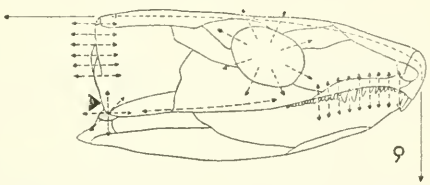

FIG. 9. *Captorhinus*. Diagram, showing some hypothetical lines of stress. Approx. × 1.

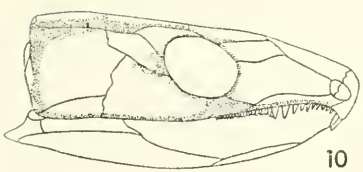

FIG. 10. *Captorhinus*. Diagram, showing areas of internal thickening. Approx. × 1.

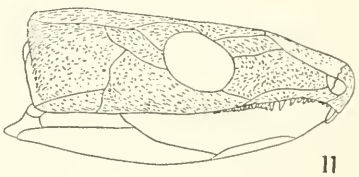

FIG. 11. *Captorhinus*. Diagram, showing orientation of sculpture. Approx. × 1.

Secondly, the vectors of mechanical force associated with the temporal region are complex (Fig. 9). Presumably it was toward a more efficient mechanism to withstand these that selection on the cheek region was operating. The simpler and more readily analyzed of these forces are:

1. The force exerted by the weight of the skull anterior to the cheek and the distribution of that weight depending upon, for example, the length of the snout in relation to its width, and the density of the bone.
2. The weight of the jaw pulling down on the suspensorium when the jaw is at rest and the compression against the suspensorium when the jaw is adducted; the distribution of these stresses depending upon the length and breadth of the snout, the rigidity of the anterior symphysis, and the extent of the quadrate-articular joint.

3. The magnitude and extent of the vectors of force transmitted through the occiput from the articulation with the vertebral column and from the pull of the axial musculature.

4. The downward pull on the skull-roof by the adductor muscles of the mandible.

5. The lateral push exerted against the cheek by the expansion of the mandibular adductors during contraction.

6. The necessity to compensate for the weakness in the skull caused by the orbits, particularly in those kinds of primitive tetrapods in which the orbits are large.

The distribution of these stresses is further complicated and modified by such factors as:

1. The completeness or incompleteness of the occiput and the location and extent of its attachment to the dermal roof.

2. The size and rigidity of the braincase and palate, and the extent and rigidity of their contact with the skull.

The stresses applied to the cheek fall into two groups. The first includes all of those stresses that ran through and parallel to the plane of the cheek initially. The weight of the jaw and snout, the pull of the axial musculature, and the necessity to provide firm anchorage for the teeth created stresses that acted in this manner. The second group comprises those stresses that were applied initially at an oblique angle to the cheek and not parallel to its plane. Within this group are the stresses created by the adductors of the jaw, pulling down and medially from the roof, and sometimes, during contraction, pushing out against the cheek.

It is reasonable to assume that the vectors of these stresses were concentrated at the loci of their origin. For example, the effect of the forces created by the articulation of the jaw upon the skull was concentrated at the joint between the quadrate, quadratojugal, and squamosal bones. From this relatively restricted area, the stresses radiated out over the temporal region. Similarly, the stresses transmitted by the occiput radiated over the cheek from the points of articulation of the dermal roof with the occipital plate. In both of these examples, the vectors paralleled the plane of the cheek bones. Similar radiation from a restricted area, but of a secondary nature, resulted from stresses applied obliquely to the plane of the cheek. The initial stresses caused by the adductors of the jaw resulted from muscles pulling away from the skull-roof; secondary stresses, created at the origins of these muscles, radiated out over the cheek, parallel to its plane.

The result of the summation of all of those vectors was a complex grid of intersecting lines of force passing in many directions both

parallel to the plane of the cheek and at the perpendicular or at an angle oblique to the perpendicular to the plane of the cheek.

Complexities are infused into this analysis with the division of relatively undifferentiated muscles into subordinate groups. The differentiation of the muscles was related to changing food habits, increased mobility of the head, and increase in the freedom of movement of the shoulder girdle and forelimbs (Olson, 1961:214). As Olson has pointed out, this further localized the stresses to which the bone was subjected. Additional localization of stresses was created with the origin and development of tetrapods (reptiles) that were independent of an aquatic environment and were subjected to greater effects of gravity and loss of bouyancy in the migration from the aqueous environment to the environment of air. The localization of these stresses was in the border area of the cheek, away from its center.

What evidence is available to support this analysis of hypothetical forces transmitted through the fully-roofed skull of such an animal as *Captorhinus*?

It is axiomatic that bones or parts of bones that are subject to increased stress become thicker, at least in part. This occurs ontogenetically, and it occurs phylogenetically through selection. Weak bones will not be selected for. Figure 10 illustrates the pattern of the areas of the skull-roof in the temporal region that are marked on the internal surface by broad, low thickened ridges. The position of these ridges correlates well with the position of the oriented stresses that were presumably applied to the skull of *Captorhinus* during life. It can be seen from Figure 10 that the central area of the cheek is thinner than parts of the cheek that border the central area. The thickened border areas were the regions of the cheek that were subjected to greater stress than the thin central areas.

External evidence of stress may also be present. The pattern of sculpturing of *Captorhinus* is presented in Figure 11. The longer ridges are arranged in a definite pattern. Their position and direction correlates well with the thickened border of the cheek, the region in which the stresses are distinctly oriented. For example, a ridge is present on the internal surface of the squamosal along its dorsal border. Externally, the sculptured ridges are long and roughly parallel, both to each other and to the internal ridge.

The central area of the cheek is characterized by a reticulate pattern of short ridges, without apparent orientation. The thinness of the bone in this area indicates that stresses were less severe here.

The random pattern of the sculpture also indicates that the stresses passed in many directions, parallel to the plane of the cheek and obliquely to that plane.

Possible Explanation for the Appearance of Temporal Openings

Bone has three primary functions: support, protection and participation in calcium metabolism. Let us assume that the requirements of calcium metabolism affect the mass of bone that is selected for, but do not grossly affect the morphology of the bones of that mass. Then selection operates to meet the needs for support within the limits that are set by the necessity to provide the protection for vital organs. After the needs for protection are satisfied, the remaining variable and the one most effective in determining the morphology of bones is selection for increased efficiency in meeting stress.

Let us also assume that bone increases in size and/or compactness in response to selection for meeting demands of increased stress, but is selected against when requirements for support are reduced or absent. Selection against bone could only be effective within the limits prescribed by the requirements for protection and calcium metabolism.

We may therefore assume that there is conservation in selection against characters having multiple functions. Since bone is an organ system that plays a multiple role in the vertebrate organism, a change in the selective pressures that affect one of the roles of bone can only be effective within the limits set by the other roles. For example, selection against bone that is no longer essential for support can occur only so long as the metabolic and protective needs of the organism provided by that character are not compromised. If a character no longer has a positive survival value and is not linked with a character that does have a positive survival value, then the metabolic demands for the development and maintenance of that character no longer have a positive survival value. A useless burden of metabolic demands is placed upon the organism because the character no longer aids the survival of the organism. If selection caused, for example, muscles to migrate away from the center of the cheek, the bone that had previously provided support for these muscles would have lost one of its functions. If in a population of such individuals, variation in the thickness of the bone of the cheek occurred, those with thinner bone in the cheek would be selected for, because less metabolic activity was diverted to building and maintaining what is now a character of reduced functional

significance. A continuation of the process would eliminate the bone or part of the bone in question while increasing the metabolic efficiency of the organism. The bone is no longer essential for support, the contribution of the mass of bone to calcium metabolism and the contribution of this part of the skeleton to protection have not been compromised, and the available energy can be diverted to other needs.

The study of *Captorhinus* has indicated that the central area of the cheek was subjected to less stress than the border areas. A similar condition in basal reptiles may well have been present. A continued trend in reducing the thickness of the bone of the cheek in the manner described above may well have resulted in the appearance of the first reptiles with temporal fenestrae arising from the basal stock.

Such an explanation adequately accounts for an increased selective advantage in the step-by-step thinning of the cheek-wall prior to the time of actual breakthrough. It is difficult to see the advantage during such stages if explanations of weight reduction or bulging musculature are accepted.

After the appearance of temporal fenestrae, selection for the classical factors is quite acceptable to explain the further development of fenestration. The continued enlargement of the temporal fenestrae in the pelycosaur-therapsid lineage undoubtedly was correlated with the advantages accrued from securing greater space to allow increased lateral expansion of contracting mandibular adductors. Similarly, weight in absolute terms can reasonably be suggested to explain the dramatic fenestration in the skeletons of many large dinosaurs.

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